

THE HOST-FINDING BEHAVIOR OF APANTELES MARGINIVENTRIS
(CRESSON) IN RESPONSE TO KAIROMONES PRODUCED BY ITS HOST,
THE FALL ARMYWORM, SPODOPTERA FRUGIPERDA (J. E. SMITH)

By

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Major Department: Entomology and Nematology

The host-finding behaviour of Apanteles marginiventris (Cresson) is divisible into 4 phases, viz., random search, non-random search, oviposition and non-search (preening and resting). Parasitoids within the host habitat were primarily influenced by short-range plant/host factors. Attraction of parasitoids, % searching time and level of parasitization were significantly higher (5% level) on fall armyworm damaged corn when compared to artificially damaged and non-damaged plants. Attraction of parasitoids, amount of searching time and level of parasitization on artificially damaged plants were greater when compared to non-damaged plants.

Reliable bioassays were developed in 10 cm petri dishes. No significant difference in response to kairomones was found between mated, 3-day old, inexperienced (no previous kairomone exposure) and experienced

(previous kairomone exposure) parasitoids. However, experienced females (with previous oviposition experience) showed the highest response while inexperienced females returned more frequently to the kairomonal spot. Virgin 4-day old females were highly responsive. No significant differences in response (high) were found in mated females ranging in age from 1-6 days. Diel response was not significantly different between 0800 to 1630 h. Removal of both apical halves and complete amputation of the antennae caused a significant reduction in response to kairomones. Parasitoids were equally responsive to kairomones from all 6 instars of the fall armyworm. First through early third instars were preferentially parasitized but older ones were attacked if immobilized.

Frass, cuticle odor and scales elicited the strongest host-seeking response. Larval silk, oral secretions and hemolymph also produced a host-seeking response. Parasitoids showed only slight differences in response to frass from fall armyworm larvae reared on various host plants. The frass produced from feeding on leaves of various host plants was more stimulatory than that produced from a meridic laboratory diet. Positive host-seeking responses were elicited from parasitoids when artificially damaged and crushed corn leaves were presented. Intact corn leaf elicited a negligible response. Consistently strong host-seeking responses were exhibited by parasitoids when stipled corn leaves were presented in combination with oral secretions, frass and cuticle odor. Kairomonal extracts from frass and corn leaves were prepared with hexane, chloroform, methanol and water. Chloroform extract of corn leaves, and the hexane and chloroform extracts of frass were the most active.

Increased parasitization was achieved by spraying kairomonal extracts onto corn plants. Plants sprayed entirely with extract yielded the highest level of parasitization (50%) while spot spraying produced significantly less parasitization (29.2%). Significantly higher percentages of parasitoid retention and fall armyworm parasitization were recorded for prestimulated parasitoids compared to unstimulated ones. Fresh frass was a better prerelease stimulant than its hexane extract. Topical treatment of non-host larvae with hexane frass extract caused a significant increase in parasitization.

INTRODUCTION

Pest control has become such an important part of modern agriculture that it is now a major requisite for the economic and successful production of food and fiber. However, some of the methods used during the past three decades have produced many undesirable effects. There is a general concurrence among crop protection workers that there is an urgent need to develop more effective and efficient methods for pest management based on sound ecological principles. Current methods may vary greatly, but they have been developed to reflect compromises involving technological capability, economic feasibility and socio-environmental acceptability. Future developments in pest control can be expected to continue to center around integrated pest management systems that emphasize the use of biological and cultural control strategies.

One important aspect of biological control that is currently receiving increased attention is the study of behavioral manipulation of natural enemies, particularly parasitoids. It is known that parasitoids find their hosts through physical and chemical cues. These cues elicit a series of directed responses that serve to reduce and restrict the area searched. According to Vinson (1976), chemical cues play a major role at almost every level in the host-finding process by releasing behavioral patterns that increase the probability of a parasitoid finding its host. Behavioral manipulation of natural enemies, such as parasitoids, has thus become a viable goal for biological control practitioners. Recent work concerning the behavior of some natural

enemies of pest insects suggests that this goal may become a reality. Experimental results have shown that interspecific semiochemicals, such as kairomones, can be exploited in various ways to enhance host-finding and parasitization (Lewis et al. 1976a,b, Vinson 1977).

The following research was conceived to investigate the host-finding behavior of Apanteles marginiventris (Cresson) in relation to the fall armyworm, Spodoptera frugiperda (J. E. Smith), a very important agricultural pest in the southeastern United States. The objectives of the study were:

- I. Description of the characteristic host-finding behavior of A. marginiventris and differentiation of this behavior from other types of non-searching behavior.
2. Biological and behavioral investigations pertinent to development of a reliable bioassay for kairomone studies of the A. marginiventris/S. frugiperda system.
3. Defining the role of plant and host substances in the host-finding behavior of A. marginiventris.
4. Extraction of kairomones/semiochemicals from substances eliciting strong behavioral responses in A. marginiventris.
5. Demonstration of some potential uses of kairomones in behavioral manipulation of A. marginiventris.

LITERATURE REVIEW

The Fall Armyworm, *Spodoptera frugiperda* (J. E. Smith)

Systematics

The fall armyworm was first described and placed in the genus Pha-laena by Smith and Abbott in 1797 (Morrill 1971). Since then, it has been placed in several genera and this early systematic history has been reviewed by Luginbill (1928). Currently, the accepted scientific name is Spodoptera frugiperda (J. E. Smith). Its accepted common name is the fall armyworm (Morrill 1971), although in the southern United States, it is unofficially called the budworm when it inhabits corn whorls.

Origin and Seasonal Distribution

This species has a tropical-subtropical origin in the Western Hemisphere (Luginbill 1928), most probably Central or South America (Morrill 1971). Spodoptera frugiperda (J. E. Smith) overwinters in Southern Florida and Texas where hosts are continually available and temperatures are seldom below 10°C. In mild winters, it also overwinters in Louisiana and Arizona (Snow and Copeland 1969). There is no record of diapause and during each growing season, the insect redisperses throughout the Eastern and Central United States and into southern Canada (Sparks 1979). Movements of individuals responsible for yearly recolonization of locations northwards of rewintering sites are not clearly understood.

Biology

Important aspects of the biology and life history of the fall armyworm have been summarized by Luginbill (1928), Vickery (1929), Sparks (1979) and Keller (1980). Adults feed, mate and oviposit at night provided the temperature is suitable. Oviposition normally takes place on host plants where as many as several hundred eggs may be laid in a mass and covered with scales. Luginbill (1928) reported that total oviposition by a female may exceed 2000 eggs over a period of up to 23 days. Vickery (1929) observed hatched larvae devouring their residual egg shells before dispersing with the aid of silken threads and the wind. As a result of positive phototactic and negative geotactic behaviors, first instar larvae move into whorls of corn and sorghum (Pitre 1979). Luginbill (1928) and Morrill and Greene (1973) reported that larvae feed preferentially first on developing leaves, then on tassels and later on ears. According to Luginbill (1928) and Keller (1980), larval development can proceed through 6, sometimes 7 and rarely 8 instars. Pupation normally occurs in the soil with a pupal chamber located 2 to 8 cm below the surface (Luginbill 1928), but during outbreaks, pupae may be found on plant parts (Burkhardt 1953). Depending on the host plant or diet, the duration of larval development, pupal size, adult longevity, fecundity and egg viability may vary significantly (Roberts 1965).

Economic Status

The species was first recorded as an injurious pest in Georgia in 1797 (Sparks 1979). Since then, Luginbill (1928) has called it an agricultural pest of the "first order" in the United States. Damaging populations of the fall armyworm appear to occur irregularly, and conditions conducive to outbreaks are not well understood (Keller 1980).

The host plants fed upon by S. frugiperda include many species in the families Poaceae and Leguminosae (Luginbill 1928, Agnello 1978). Some 57 plant species are listed and many of these are economically important field, vegetable and forage crops, such as corn, sorghum, peanuts, rice, soybeans, alfalfa and bermuda grass. Average estimates of annual crop losses caused by the fall armyworm exceed \$300 million (Mitchell 1979).

Types of damage reported to be caused by S. frugiperda are defoliation, whorl damage, ear and tassel damage, death of plant and promotion of entry of plant pathogens. Defoliation ranges from skeletonization of leaves by early larval instars to complete consumption of entire leaves by large larvae. Morrill (1971) reported that additional damage can be caused to developing ears such as incomplete fertilization and setting of kernels due to larvae feeding on the silk and tassels.

Natural Mortality

Natural mortality of fall armyworm populations in the field is brought about by various abiotic and biotic agents. Among the abiotic environmental factors, temperature appears to be an important limiting factor. Luginbill (1928) and Wood et al. (1979) documented low temperature as probably the most important factor limiting the winter survival of S. frugiperda. At 15.6°C or below, no egg hatch occurred, while a high temperature of 37.8°C prevented complete larval development (Barfield et al. 1978). Pupae exposed to soil temperatures of 38°C may be killed in less than 0.5 hour (Luginbill 1928).

The impact of cannibalism on fall armyworm population dynamics is not fully understood. However, Wiseman and McMillian (1969) found that mortality attributable to cannibalistic activity and intraspecific com-

petition is positively correlated with larval density. Olive (1955) believed that mortality in populations can also occur as a result of damage to adjacent, unhatched eggs by newly-hatched larvae chewing on these eggs while in the process of devouring their own residual egg shells.

A multitude of natural enemies (parasitoids, predators and pathogens) are known to attack the fall armyworm in the field (Luginbill 1928, Agnello 1978, Ashley 1979 and Keller 1980). Arthropod natural enemies are the most important, and parasitoids as a group exert the most consistent and significant influence on fall armyworm mortality. Agnello (1978) and Ashley (1979) listed over 70 species of parasitoids (4 families of Diptera and 8 families of Hymenoptera) as having been reared from immature stages of S. frugiperda. The spectrum and importance of parasitoid species attacking fall armyworm immatures vary between agroecosystems. For example, in a study by Ashley et al. (1980), 8 species of parasitoids were reared from larvae feeding on corn and surrounding broadleaf signalgrass weeds, with Chelonus texanus Cresson, Meteorus autographae Muesebeck and Euplectrus platyhyphenae Howard inflicting the highest mortality. However, Nickle (1977) attributed parasitization of fall armyworm larvae feeding on peanut foliage to 7 species, and Apanteles marginiventris (Cresson), M. autographae and Ophion sp. were responsible for the highest mortality. Furthermore, Mueller and Kunna-laca (1979) reported that importance of a particular parasitoid species of the same pest in the same crop can vary depending on locality of the cropping system. Variation of parasitoid complex can also be influenced by kinds of alternate host populations and accompanying plant species present (Tingle et al. 1978).

Other natural enemies which play a somewhat lower and less consistent role in the regulation of fall armyworm populations are various predators and pathogens. Ten species of Hymenoptera (8 vespids and 2 sphecids), 6 Hemipterans (1 anthocorid, 1 nabid, 1 pentatomid, 3 reduviids), 11 Coleopterans (9 carabids, 2 cicindellids, 1 sp. of coccinellid), a mammal (skunk), 3 amphibians (2 Bufo spp. and 1 Hyla sp.), and a variety (13 species) of birds have been listed as predators of S. frugiperda by Agnello (1978). Agnello (1978) also compiled a list of 7 bacterial, viral and fungal pathogens that have been known to attack the fall armyworm. Keller (1980) further reported Nomuraea rileyi (Farlow) Sampson, a fungus, as being pathogenic to field larvae.

Control Measures

Major management practices for control of fall armyworm are presently restricted to pesticide application (Young 1979) and cultural controls (Luginbill 1928). Investigation of additional control measures is currently being evaluated. Wiseman and Davis (1979) have shown that host plant resistance may be of potential use. Other biological methods such as the use and the manipulation of natural enemies have yet to become significant components of an integrated management program (Ashley 1979). There is an obvious lack of detailed information on the multitude of natural enemies mentioned earlier, and current published fall armyworm data are either too general or too few to allow the derivation of pest management and population dynamics models representative of fall armyworm-host-plant interaction.

The Larval Endoparasitoid, Apanteles marginiventris (Cresson)

Among the vast number of natural enemies attacking fall armyworm larvae in various regions and countries, Apanteles marginiventris (Cresson) is one of the most frequently recovered parasitoids from field collected fall armyworm larvae, the other being Chelonus texanus (Cresson) (Ashley 1979).

Origin and Distribution

A. marginiventris (Cresson), originally described from Cuba, is native to the West Indies (Muesebeck 1921). It has been previously named as Microgaster marginiventris Cresson (1865), Apanteles grenadensis Ashmead (1900), A. laphygmae Ashmead (1901) and Apanteles (Prota-panteles) harnedi Viereck (1912). This parasitoid has been reported from various countries, namely, Colombia, Cuba, Mexico, Uruguay, United States of America, Venezuela and the West Indies (Wilson 1933, Marsh 1978, Ashley 1979 and Danks et al. 1979). Within the United States, it appears to have a wide distribution, at least seasonally, in the southern states, viz. Arkansas, Florida, Georgia, Louisiana, Mississippi, Tennessee, North Carolina and South Carolina (Wilson 1933, Mueller and Kunnalaca 1979). Its range also extends through Oklahoma, Kansas, Wisconsin, Texas, Arizona, California and Hawaii (Marsh 1978).

Description

The egg and larval stages have been described in some detail by Boling and Pitre (1970). The egg is hymenopteriform with rounded ends. The caudal end has a slightly curved, short peduncle. The first instar larva is white and caudate. The second instar differs greatly from the first in being vesiculate with a very prominent caudal vesicle. The

third instar is hymenopteriform with no caudal vesicle. The pupa is exarate and is protected by a cocoon (3 mm long) of firm, smooth, white silk. Boling and Pitre (1970) reported that cocoons from hosts other than Heliothis spp. may be yellow in color. Muesebeck (1921) described the adult (2-2.5 mm long). Identification of adults can be made using the keys of Marsh (1971) (to genus) and Muesebeck (1921) (to species). Useful diagnostic characteristics were also given by Marsh (1978) to distinguish the adult of this parasitoid from other braconids.

Biology

A. marginiventris is an arrhenotokous larval endoparasitoid of several lepidopterous pests that attack a variety of important agricultural crops. Under laboratory conditions, Boling and Pitre (1970) observed that female parasitoids were ready to mate and oviposit within several minutes after eclosion but were more aggressive when held for 24 hours prior to exposure to each other and hosts. Both sexes were observed to mate many times and freely with other individuals. Females also often mated after initiating egg laying, and no distinct pattern of ovipositing could be detected.

The egg is laid in the early instars of hosts. One to 3-day old (first and early second) instars are preferred for most of the hosts studied (Vickery 1929, Boling and Pitre 1970, Lingren 1969, Kunnalaca and Mueller 1979). Later instars are less preferred because these larvae usually react more violently when attacked (Kunnalaca and Mueller 1979). Also, they may be able to defend themselves by ejection of oral secretion or biting at the ovipositing female parasitoid. Oviposition is accomplished quickly with a single ovipositor thrust and parasitization occurs primarily during daylight hours (Kunnalaca and Mueller 1979).

Oviposition has been observed to go on for several days (Boling and Pitre 1970, Lingren 1969, Kunnalaca and Mueller 1979). Results reported vary from 4 to more than 11 days. Kunnalaca and Mueller (1979) reported that females appeared to parasitize more hosts on the second and third days. It was also observed that very few female progeny were produced after the 11th day of oviposition (Lingren 1969). Total fecundity can range from 31 to 124 eggs per female (Lingren 1969, Kunnalaca and Mueller 1979).

Superparasitization was commonly observed when few hosts were offered (Boling and Pitre 1970, Kunnalaca and Mueller 1979). For example, up to 7 eggs were found in a single host exposed to several female A. marginiventris. However, the norm is 1 egg per host and only occasionally 2 eggs per host were observed from field-collected larvae (Boling and Pitre 1970). Superparasitization does not necessarily lead to multiple cocoon formation. When multiple cocoon formation was observed, the general number was 2 per host but 3 were sometimes produced from bollworm larvae, especially if these larvae were exposed when they were 3 days old or older (Lingren 1969).

The time required for the development of A. marginiventris from oviposition to cocoon formation ranged from 6 to 11 days at 30°C (Wilson 1933, Boling and Pitre 1970, Danks et al. 1979, Kunnalaca and Mueller 1979). Optimal development time varied between host species. Boling and Pitre (1970) reported an optimum time of 7 days in Trichoplusia ni (Hubner) and Pseudoplusia includens (Walker), and 6 days in Heliothis virescens (F.). In Plathypena scabra (F.), 8 days was the optimum development time (Kunnalaca and Mueller 1979). At 30°C, development times for both sexes were the

same, while at 25°C, females required a slightly longer period (Kunnalaca and Mueller 1979). Mated females generally produced progeny of approximately 1:1 sex ratio (Boling and Pitre 1970). Mean longevity for adults at 30°C was 5.6 ± 2.5 days and females generally lived longer than males (Kunnalaca and Mueller 1979).

Numerous lepidopterans are attacked by A. marginiventris. Some 16 hosts have been reported (Thompson 1953, Lingren 1969, Miller 1977, Wall and Berberet 1975). All the hosts attacked are noctuids. No crop preference was shown by parasitoids attacking I. ni on various food plants in Mississippi (Boling and Pitre 1970).

Kairomones and Host-Finding by Parasitoids

Female parasitoids often emerge in a habitat lacking the proper hosts. These females then seek out a suitable environment (Salt 1935, Douth et al. 1976). Laing (1938) believed that the female parasitoid is guided to a host habitat by chemical and physical parameters. The location of the proper hosts is so critically important for successful parasitism that many parasitoids have evolved mechanisms which enable them to detect and orientate to hosts from a distance. This ability has been called host location or host-finding and is defined as the perception and orientation by parasitoids to their hosts from a distance by response to stimuli directly associated with their hosts or host products (Weseloh 1981).

Based on the observations of Salt (1935) and Flanders (1953), Douth (1964) divided the process that results in successful parasitism into 4 steps, viz. host habitat location, host location, host acceptance and host suitability. Vinson (1975a) considered the first 3 steps

to be integral components that can be collectively referred to as the host selection process. He proposed a fifth step and called it host regulation.

Host Selection Strategy

It has been suggested that hosts of parasitoids are found through random searching, particularly once a suitable habitat has been located. Many models of host location reflect this idea. Evidence has also been gathered showing that once the host area is located, searching is not completely random but is modified through the discernment of host-related cues. Others have also suggested that the searching behavior of many parasitoids was somewhere between that of a random search and a systematic one (Vinson 1977).

Many parasitoids appear to locate their hosts through a sequence of steps. Some parts of the host selection process of some parasitoids may indeed involve a sequence of cues. These cues can follow one another, each leading the parasitoid closer to the host. Vinson (1968) observed that Cardochiles nigriceps Viereck is first attracted to the host plant of its host, H. virescens. Once in the proper plant habitat, females orientate to the host plants and fly from plant to plant, searching each in turn by flying 2 to 5 cm from the stems, leaves and buds. Females alight briefly and antennate damaged plant tissues, and may then resume their search. However, if the damage was inflicted by a potential host, the female parasitoid crawls over the plant and rubs the surface with her antennae. Although one cue may lead to another and bring the parasitoid closer to its host at each step, any given cue may only elicit the proper response in the presence of essential preceding cues. Thus, the parasitoid may be led to a host

through a hierarchy of cues emanating from the host's immediate environment, and different stimuli or different concentrations of a single stimulus may be involved (Vinson 1977). Ultimately, whether the female parasitoid responds to a series of independent cues or a hierarchy of cues, each succeeding step serves to reduce the distance between it and its host, thereby increasing the potential for encounter.

While some parasitoids are capable of following a continuous trail leading to a host, a continuous trail is not always necessary. When a female parasitoid encounters a stimulus, she searches for the next but within the context of the present or last stimulus. Some stimuli release an innate searching behavior in certain parasitoids. Females encountering a chemically-contaminated surface will not only search the contaminated surface, but also adjacent areas. Vinson (1977) observed that Microplitis croceipes (Cresson) upon contacting frass of its host, H. zea, placed on a leaf, will crawl all over the leaf while antennating the surface. The female parasitoid may return to the frass or search the underside of the leaf and adjacent stem before leaving. In studies involving Trichogramma sp. and M. croceipes, Lewis et al. (1975) reported that parasitization was greater in areas adjacent to those treated with chemicals isolated from the host.

It is currently accepted that many insect parasitoids appear to be directed to their hosts through a series of physical and chemical cues. These cues elicit a series of directed responses by the female parasitoid that serve to reduce and restrict the area and habitats searched, and the species of hosts thus located. According to Vinson (1976), these factors may become increasingly refined in the more host-specific parasitoids. Several host selection strategies of parasitoids

in addition to the above-mentioned ones are known and the evolution of all these strategies appear to be related in part to the specificity of the parasitoid-host association (Vinson 1977).

Role of Chemicals in Host Selection

Various kinds of stimuli have been found to be important in host selection. Physical stimuli such as color, sound, shape, texture and movement do not appear to show great promise in the augmentation or manipulation of entomophagous arthropods (Vinson 1976). However, chemicals appear to play a significant role at almost all levels of the host selection process by releasing behavioral patterns involved in host selection, particularly among the parasitic hymenopterans.

Brown et al. (1970) have defined chemicals involved in host selection on the basis of their origins and the behavioral response which they elicit. Nordlund and Lewis (1976) reexamined the terminology and proposed two additional classes of interspecific semiochemicals (synomones and apneumones). They defined a kairomone as being a chemical produced or acquired by an individual of one species, which when contacted by an individual of another species in the natural context, evokes in the receiver a behavioral or physiological response adaptively favorable to the receiver. A number of kairomones have been isolated and identified (Jones et al. 1971, Jones et al. 1973, Hendry et al. 1973, Vinson et al. 1975, Henson et al. 1977 and Greany et al. 1977). Many more have been studied but have not been identified. In general, the findings indicate that such chemicals are diverse and the types of behavioral responses elicited by these chemicals differ considerably (Vinson 1977).

To be effective in orientating a parasitoid in host habitat location, chemicals involved have to possess a degree of volatility. Potential sources of such chemicals are the food plant of the host, non-host organisms associated with the host habitat and the host itself. Olfactometer studies have shown that several species of hymenopterous parasitoids were attracted to odors from the food plants of their hosts (Vinson 1977). Vinson (1975a) reported that C. nigriceps appeared to cue first on plant factors, but once in the proper habitat, it cued on injured plant tissues. Terpenes released by pine trees injured by the southern pine beetle were observed to influence the sequence of arrival of parasitoids (Camors and Payne 1973).

In some parasitoid-host relationships, organisms in association with the host are apparently responsible for providing cues to the host's habitat. For example, Greany et al. (1977) observed that acetyldehyde and ethanol produced by the fungus, Monolinia fructicola (Wint.), in rotting peaches occupied by Anastrepha suspensa (Loew.), attracted Biosteres longicaudatus (Ashmead) to the host habitat.

Odors from the host itself may provide the necessary cues too, for habitat and host location. The orientation of a parasitoid to host-liberated volatile chemicals might be expected in situations in which the stage that releases the odor is either attacked directly or occurs with the appropriate host stage. Lewis et al. (1971) reported that chemicals deposited during oviposition by H. zea stimulated searching by Trichogramma evanescens Westwood. Vinson (1975b) observed a similar case involving C. texanus, an egg-larval parasitoid of H. virescens. Vinson (1977) also reviewed cases which documented that some parasitoids are also responsive to pheromones produced by their hosts.

Host location follows host habitat location and is primarily mediated by short range or contact chemicals. These chemicals may be derived directly from the host or from the host's plant food. Female parasitoids contacting these chemicals may orient towards and be led to the host, but many of these chemicals actually act as searching stimulants rather than as attractants (Vinson 1977). These compounds release an intensified searching behavior involving a more restricted area than that released by the previous cues (Vinson and Lewis 1965, Vinson 1975b). Many cases documenting the study of short range or contact chemicals have been reviewed by Vinson (1976). The chemistry of several contact chemicals has been worked out and several of the compounds are high molecular weight hydrocarbons, supporting the view that these compounds are of low volatility (Jones et al. 1971, Jones et al. 1973, Vinson et al. 1975).

Sources of Host Kairomones (Searching Stimulants)

There are several sources within a host from which kairomones have been detected. Most host kairomones are not limited to just one location or source in the host. However, in cases of more than one active component, the optimum mixture may be concentrated in one organ, tissue or host substance (Jones et al. 1976, Lewis et al. 1976a). For example, gas chromatographic data showed the presence of similar hydrocarbons with dissimilar ratios in samples of mandibular gland, cuticle, hemolymph and frass of several lepidopteran larvae (Jones et al. 1976). In the situation involving different parasitoids of the same host, the source and chemical nature of the kairomone(s) may differ. As an example, the case of H. virescens is reviewed. H. virescens serves as a host for several parasitoid species. Nettles and Burks (1975) found

that a tachinid parasitoid, Archytas marmoratus (Zeller), was stimulated to larviposit by a protein in the frass of H. virescens. Jones et al. (1971) observed that M. croceipes was stimulated to search by a hydrocarbon found in the frass. C. nigriceps, on the other hand, is stimulated to search by mandibular gland secretions (Vinson 1968). Wilson et al. (1974) and Schmidt (1974) observed that Campoletis sonorensis (Cameron) could be stimulated by frass and cuticle. Lastly, egg parasitoids, such as I. evanescens and C. chelonus, were influenced by chemicals from the female Heliothis moth and the egg chorion.

From the literature reviewed, it appears that cuticle, mandibular and labial gland secretions and particularly frass are the commonly encountered sources of kairomones utilized by parasitoids in host-finding. It is interesting to note that parasitoids have been reported to also use host pheromones to aid in host location. Venturia (Nemeritis) canescens (Gravenhorst) is stimulated by the dispersal pheromone (mandibular gland secretion) of Anagasta (Ephestia) kuehniella (Zeller). The host-marking pheromone of Rhagoletis pomonella (Walsh) is attractive to and elicited ovipositor probing of the infested cherry by Opius lectus Gahan. There are also several cases reported where the host's sex pheromones attracted their parasitoids (Vinson 1977).

Behavioral Responses of Parasitoids to Kairomones

There are a number of different types of behavioral patterns that may be elicited by allelochemicals (e.g. kairomones) depending on the parasitoid species and host involved as well as the level of the host selection process.

The response of parasitoids from a distance to hosts as mediated by chemicals can most conveniently be divided into 2 categories:

olfaction and contact chemoreception. Both olfaction and chemoreception are important in host location. They are not absolutely distinct, for olfaction grades into contact chemoreception as the distance between receptor and sources becomes less and less (Weseloh 1980).

Air-borne compounds may elicit activity in the parasitoid, stimulating it to fly or crawl upwind or only to orientate to the odor source. It is possible that anemotaxis and/or chemotaxis as outlined by Shorey (1973 and 1976) is operative in the orientation behavior of parasitoids responding to olfaction of air-borne chemicals. If host odor is perceived over only a short range, the parasitoid may make numerous turning movements (klinotaxis).

Contact chemoreception usually elicits an antennation response (Vinson 1977). Waage (1978) described in some detail the behavioral changes of a parasitoid contacting host chemicals. He found that when a parasitoid touches a contact chemical stimulus, it usually reduces its walking speed or stops (an inverse orthokinetic response). As it examines the substrate, it also increases its rate of turning which may either be in a random direction (klinokinesis) or oriented with respect to the geometry of the chemical "patch" (klinotaxis). Waage also showed that parasitoids tend to make directed 180° turns at patch edges which serve to orientate them back into the chemical spot. This "examination behavior" functions to retain the parasitoid on a chemical patch and also insures that the patch will be explored thoroughly.

Vinson (1977) observed that the female parasitoid's antennae usually move alternately up and down, occasionally touching the substrate as the parasitoid moves about. Upon contacting a host or traces

of a host, the antennae rub and palpate the object. The object or contaminated substrate is intensely antennated, followed by examination of the immediate area round it. In some cases, antennal drumming occurs, especially in Chalcidoidea which have "elbowed" antennae (Edwards 1954).

Antennal response is often followed by other behavioral responses related to oviposition. Tucker and Leonard (1977) described various responses of Brachymeria intermedia (Nees) to its hosts. Following antennal contact, various responses observed were antennal drumming, mounting, grasping, drilling, piercing and oviposition. Such responses are commonly seen in various other hymenopterous parasitoids.

Certain tachinids when contacting host kairomones respond to larviposition. Nettles and Burks (1975) observed that Archytas marmoratus was stimulated to larviposit on contact with host frass. Roth (1976) observed the same response in Lixophaga diatreae (Townsend), a parasitoid of the sugarcane borer, Diatraea saccharalis (F.). In both cases, sensing the kairomones was by contact via the fore-tarsi.

Potential Uses of Kairomones

Since the time of Wright (1965) who recognized the potential for pest management by the behavioral modification of insects through the use of non-toxic agents that modify the insect's behavior, much effort has been underway to develop methods of manipulating pest insects. However, a different approach is needed for the manipulation of natural enemies. Instead of attempts to elicit an incorrect response or inhibit a correct one, the goal of entomophagous insect manipulation is to redirect an incorrect response or stimulate the correct one. The behavioral modification of certain arthropod enemies of insect pests

through the use of chemicals (e.g. kairomones) has provided new opportunities for the manipulation of these arthropods for the benefit of man. Such a pest control tactic is compatible with current pest management philosophies and fits well into an IPM scheme which often has to reflect compromises involving technological capability, economic feasibility and social acceptability.

The potential uses that have been proposed for parasitoid kairomones are:

1. Stabilization and activation prior to field release (Pre-release stimulation).
2. Activation and retention in the release area (Plot treatment).
3. Improved egg distribution.
4. Oviposition in artificial substrates for in vitro rearing.
5. Increasing longevity and total productivity.
6. Acceptance of factitious hosts to enhance research and laboratory rearing.

Lewis et al. (1975) reported that % parasitization by Trichogramma of H. zea eggs was higher in pans of pea plants uniformly treated with tricosane (a kairomone) than on control plants. Parasitization in partially treated pans of pea plants was intermediate between completely treated and nontreated plants. Their results suggest that the parasitoid is activated or stimulated by the kairomone to search and is retained in the "search and attack" cycle by continual reinforcement. The stimulants appear to cause the parasitoids to search contaminated as well as areas adjacent to contaminated areas.

Kairomones appear to retain parasitoids in contaminated areas. Lewis et al. (1975) observed that released M. croceipes females were

retained on pea plants which contained hosts as well as on plants lacking hosts but contaminated by frass and feeding damage. On the other hand, released parasitoids deserted the pea seedlings that had no host or host products. By applying kairomones to plants having a low density of hosts, the parasitoids can be activated and retained. This retention and activation increases the chance for host contact and results in greater parasitization.

A blanket coverage by a kairomone might lead to improved egg distribution. In the presence of a blanket treatment, the female would be stimulated to search and would more likely be led away from a host that was just attacked. Such a situation has been reported by Lewis et al. (1975).

Successful establishment and retention of entomophagous insects released in target areas are highly important. One of the problems frequently encountered is that upon release, many entomophagous insects rapidly disperse, being carried by wind or flying away from the release site. Gross et al. (1975) used kairomones as sign stimuli (releasers) to place the parasitoids in the "host-finding and attack cycle", thus reducing the tendency of the parasitoid to enter the escape and dispersal behavior phase. Another aspect of parasitoid behavior that may play an important role in manipulation of these beneficial insects is the concept of associative learning. Vinson et al. (1977) and Arthur (1971) demonstrated that some parasitoids can associatively learn certain cues involved with host location which may be of further importance with regard to the prestimulation concept.

Kairomones can affect parasitoid longevity and total productivity. Ashley et al. (1974) found that Trichogramma pretiosum Riley females

lived longer when provided naturally deposited H. zea eggs as hosts than when provided naturally deposited I. ni eggs for hosts. They suggested that the difference may be have resulted from different stimuli received by the ovipositing parasitoid. Studies by Nordlund et al. (1976) demonstrated that daily level of parasitization and total progeny produced were higher in I. pretiosum which has been offered host eggs treated with a kairomone (host moth scale extract) than those offered untreated eggs.

SECTION I
HOST-FINDING BEHAVIOR OF APANTELES MARGINIVENTRIS
(CRESSON) AND INFLUENCE OF PLANT/HOST FACTORS

Introduction

The fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith) is an important annual defoliator causing economic damage to corn and Bermuda grass in the southeast and central United States. In years of high population density, FAW larvae may cause over \$300 million in damage (Mitchell 1979). The persistent abundance of this agricultural pest during the past several years has increased efforts to achieve a more comprehensive understanding of its ecology so that effective control strategies can be developed and implemented. One of the most promising approaches under consideration is the augmentation and manipulation of its natural enemies.

Apanteles marginiventris (Cresson) is one of the most frequently recovered parasitoids from field collected FAW larvae (Ashley 1979). This solitary, larval endoparasitoid appears to be an important natural enemy because it normally attacks first and second instars of the fall armyworm larvae in young corn fields and kills these larvae when they reach the third instar. Food consumption by parasitized larvae is reduced ca. 2.6 times and prevention of larval development beyond the third and early fourth instar greatly reduces the economic damage inflicted by this pest (Ashley unpublished data).

The above-mentioned biological characteristics make this parasitoid a reasonable candidate for additional research on augmentation and manipulation. One of the ways A. marginiventris could be made more effective would be through controlled management of its field activity. However, before this can be done, it is necessary to understand its host-finding behavior and to clearly define those steps in the host-finding sequence in which chemical stimuli play a major role. The following study was undertaken to describe the characteristic host-finding behavior of A. marginiventris and to define the role of plant/host chemicals in host location and to demonstrate their effects on parasitization rates.

Methods and Materials

Rearing of Experimental Insects and Planting of Corn

Young FAW larvae were obtained by incubating egg masses (deposited on Scott paper towels) in plastic containers (7.5 cm ht, 10 cm diam) containing cubes (3x3x2 cm) of a laboratory-prepared pinto bean diet (King and Leppla 1981). Egg incubation as well as parasitoid and FAW larval rearing were done in a controlled-environment cabinet set at 27°C, 70% RH and 14 h photophase. A metal grid composed of 2 pieces (5x9 cm) of 0.6 cm hardware cloth arranged in an "X" configuration was placed in each container to provide additional surface area for FAW larvae in order to reduce cannibalism.

Apanteles marginiventris progeny were reared using first instar FAW. The same plastic containers used for egg incubation also served as ovipositional units. Each unit contained a metal grid, 4 cubes of diet, ca. 100 FAW larvae, a drop of honey for parasitoid nutrition and

2 female parasitoids. The female parasitoids were obtained from a general emergence cage in which they had been exposed to males for at least 24 h prior to transfer (CO_2 used) to the ovipositional units. The units were checked daily and any unparasitized (larger) larvae were discarded. Parasitoid cocoons were harvested on the ninth day after set-up and transferred to an eclosion and holding cage made of plexiglass. This cage contained water and honey for parasitoid sustenance.

Corn plants (P-A-G hybrid) were grown in 15 cm diam and 14.5 cm high plastic planter pots in a greenhouse. The planting medium consisted of a 1:2:2 sand, perlite, peat moss mixture and supplemental nutrients were supplied by fertilizer granules (8:8:8+T.E.).

Description and Analysis of Host-Finding Behavior

Ca. 20 second instar FAW larvae were randomly placed on a 3-week old corn plant. The corn plant, placed in a plexiglass cage, was exposed to FAW feeding for 24 h before subsequent utilization. A mated, 2 to 4-day old female A. marginiventris was introduced onto the corn plant and her behavior observed under a 2x20 watt fluorescent light. Twenty females were observed and the behavioral responses recorded and synthesized to note common behavioral sequences. (4)

Attraction of Parasitoids

The attraction of mated A. marginiventris females to different types of damage on 3-week old corn plants was observed in a controlled environment cabinet. The corn plants studied were either not damaged, artificially damaged or FAW-damaged. Artificial damage was inflicted on corn leaves (to approximately the same degree as FAW damage) by stippling with a pin and puncturing with a hole-puncher. FAW damage was (4)

inflicted by allowing 20 second instar larvae to feed on the plant for 24 h after which the larvae were removed. The experiment was conducted by arranging the corn plants in the pattern shown in Fig. 1. Twenty female parasitoids were released from a plastic container placed in the center of the triangular arrangement. Temperature and humidity conditions in the cabinet were 27°C and 70% RH. Light was provided by two 20-watt fluorescent bulbs. Observations were taken every 5 minutes for 1 h. The total number of parasitoids present and the number searching on each type of corn plant were recorded for each observation. The experiment was repeated 3 times and each time the arrangement of the corn plants was changed so as to eliminate any position bias.

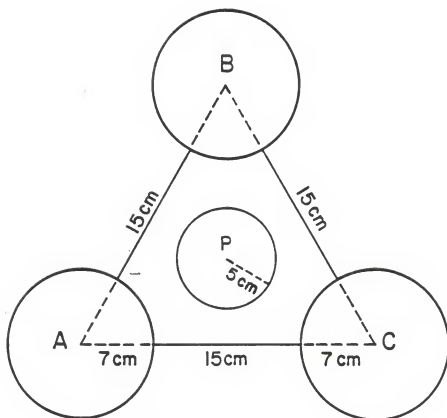
Modification of Behavior

The corn plants were prepared as in the previous experiment and placed into a plexiglass cage. A female A. marginiventris was introduced onto the corn plant and her activities observed and timed over a maximum duration of 5 minutes. A stop clock and 2 stop watches were used. This procedure was replicated 25 times.

Effect on Level of Parasitization

The design and plant preparations for this experiment were similar to those described for the attraction experiment. Thirty second instar FAW were randomly placed on each corn plant. Twenty female parasitoids were released in the center of the triangular arrangement (Fig. 1) and observations were taken at 5 minute intervals for 1 h. The number of parasitoids present and searching on each plant was recorded. The pots containing the corn plants were placed on a large sheet of white paper to facilitate recovering any FAW that had dislodged themselves during

Fig. 1. Experimental arrangement of corn plants used to observe the attraction of A. marginiventris females to different types of plant damage.



Corn Plants A - No damage
 B - Artificial damage
 C - FAW damage
P - Parasitoids released

the course of the experiment. The soil surface and sides of the pots were also carefully scanned to recover dislodged FAW larvae. All larvae were removed at the end of 1 h and dissected for determination of parasitization. The experiment was repeated 4 times, changing the arrangement of pots each time to reduce bias.

Results and Discussion

The host-finding and behavioral sequence for oviposition of A. marginiventris on FAW-damaged corn plants is presented in Fig. 2.

This sequence consists of 12 or more steps and is supported by one of the host selection strategies postulated by Vinson (1977). Preening can occur as a step at various points within the sequence as seen in the ethogram. A typical pattern involves the following steps:

1. Random movement: On undamaged portions of the corn plant, the parasitoid walks rapidly with antennae straight at 45-60° angle to the substrate. Large areas are covered in a relatively straight path.
2. Orientation: The parasitoid waves its antennae, alternating them in an up and down fashion. Leaf edges appear to be favored as the track of movement.
3. Chemotaxis: The parasitoid responds to an odor gradient by increased orthokinesis (walking) and oriented flying to the approximate site of the stimulus source.
4. Contact damage: When contact with damaged plant areas is made, locomotion is arrested and the parasitoid becomes visibly excited. Intense investigative behavior begins.
5. Antennal palpation: The parasitoid palpates the damaged areas.

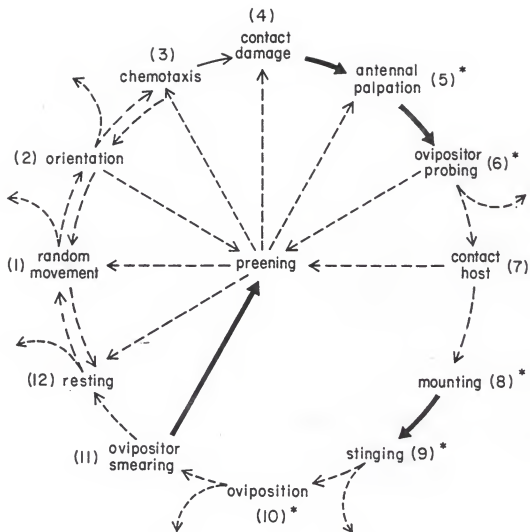
This typically involves sweeping, rubbing and tapping the damaged substrate with both antennae. Only the apical halves of the antennae appear to be used in palpation. Adjacent areas and the top and bottom surfaces of leaves are searched.

6. Ovipositor probing: In conjunction with antennal palpation and intense klinokinesis, the parasitoid is observed to arch its abdomen and rapidly probe with its ovipositor. Its wings are semi-extended and sometimes rapid fanning occurs. The parasitoid is observed to favor shot-holes and crevices made by host-feeding.
7. Host contact: Hosts are usually contacted with the tips of the antennae.
8. Mounting: This is quickly accomplished by jumping on or at the host, usually towards the posterior half of the host.
9. Stinging: Stinging is quickly executed using the ovipositor with the abdomen arched and the wings out-stretched.
10. Oviposition: This normally occurs concurrently with the stinging process. There is no wound-feeding after oviposition. The parasitoid usually moves away quickly or may even drop from the substrate or fly away. Mounting, stinging and oviposition usually requires ca. 1-3 seconds.
11. Ovipositor smearing: This involves dragging the abdomen and ovipositor on the substrate. This smearing motion is probably a means for cleaning the ovipositor. Preening always follows this behavior.
12. Resting: This is a sedentary phase in which the parasitoid is motionless.

The whole sequence outlined above can be divided into 4 phases, viz. random search, non-random search, oviposition and non-search. The

Fig. 2. Behavioral ethogram of the host-finding and ovipositional sequence of A. marginiventris on FAW-damaged corn plants.

solid arrows	= invariable pathways
dashed arrows	= variable or alternative pathways
asterisked steps	= locations where sign stimuli are involved



intensity of the random search phase is governed by appetitive behavior of endogenous origin. Non-random search or the investigative behavior phase is largely influenced by sign stimuli perceived through the sense organs. The non-random search (steps 4, 5, 6 and 7) and oviposition phases (steps 8, 9, 10 and 11) constitute what Lewis et al. (1976a,b) and Vinson (1977) have termed as the "find and attack" cycle. Analysis of the cycle showed that there are key points in which fixed-action patterns, mediated by releasing stimuli are evoked (marked with an asterisk on the ethogram). Antennal palpation and ovipositor probing are of particular interest because these actions are released primarily by contact chemical cues or chemical cues in conjunction with physical ones (eg. shot-holes and crevices). The identification of these key points within the 'find and attack' cycle is of great importance because the ability to manipulate behavior at selected points in the host-finding sequence must be achieved if more effective utilization of many parasitoids in pest management programs is to be realized.

The results of studying the attraction of parasitoids to healthy and damaged corn plants shows that FAW-damaged corn plants attracted the highest % (46.7) of released A. marginiventris and undamaged corn plants the lowest (6.7%) (Fig. 3). A similar situation was observed with regard to % parasitoids searching (Fig. 4). FAW-damaged corn plants had ca. 20% more searching parasitoids. Comparison of these 2 figures illustrates that artificially damaged corn played a more substantial role in attraction than it did in eliciting searching behavior.

Corn plant damage significantly affected the type of behavioral patterns of A. marginiventris. The % time searching was ca. 5 times greater on the FAW-damaged plants than on the artificially damaged ones,

Fig. 3. Attraction of *A. marginiventris* females to different types of corn plant damage (FAW larvae not present).

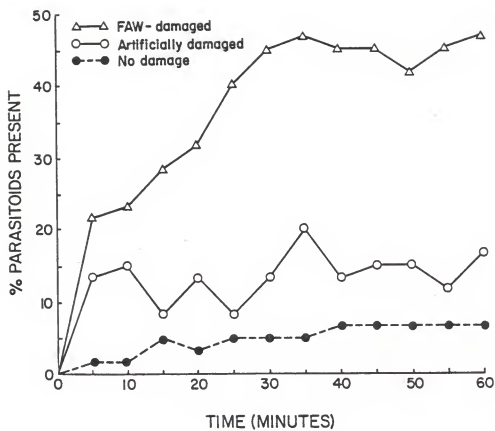
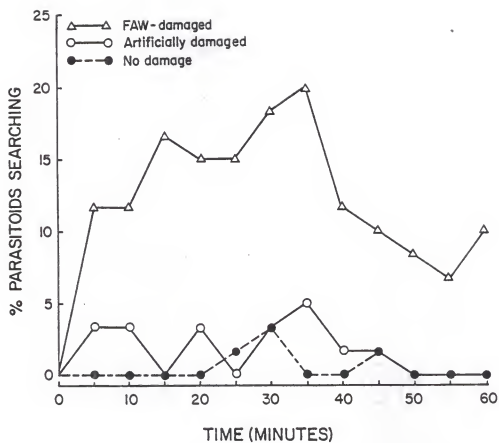


Fig. 4. Effect of different types of corn plant damage on searching by A. marginiventris females (FAW larvae not present).



and it was 33 times greater when compared to the nondamaged plants (Table 1). Resting and preening behaviors were greatest on nondamaged plants. The differences between walking and flying times were not significantly different on the 3 types of corn plants. These differences could be explained by the fact that proper and sustained responses by parasitoids are usually elicited by succeeding cues being perceived in the presence of preceding ones. This is the situation with FAW-damaged plants where all the necessary cues are present in their proper context.

Table 2 shows the results of parasitization of FAW larvae by A. marginiventris as a function of plant damage. Overall parasitization was significantly higher on FAW-damaged plants when compared to artificially-damaged and undamaged plants. The difference between overall % parasitization on artificially damaged and undamaged plants was also significant. Superparasitization occurred on FAW-damaged and artificially damaged plants but not on undamaged plants. This condition could be attributed to the presence of more parasitoids and greater searching activity on damaged plants (Figs. 5 and 6). Comparing the data in Fig. 3 and 4 with Fig. 5 and 6, it appears that the presence of host larvae did not cause any appreciable differences in the percentages of parasitoids attracted to or searching on the corn plants. This indicates that parasitoid attraction to the plants is not dependent on the presence of hosts but is dependent on whether appropriate chemical cues (plant and/or host-related) are being emitted from the plants and perceived by the parasitoids. This is similar to an observation involving attraction of Cardiochiles nigriceps Viereck to tobacco plants reported by Vinson (1975a).

Table 1. Effect of plant damage on mean % (\pm SE) time spent by A. marginiventris engaged in various searching and non-searching activities.

Activity	Type of plant damage		
	None	Artificial	FAW
Searching	2.5 \pm 0.3a	17.4 \pm 2.3b	83.2 \pm 1.2c
Resting	58.6 \pm 4.6a	54.2 \pm 2.9a	4.4 \pm 0.6b
Preening	28.8 \pm 4.7a	18.0 \pm 2.5b	6.4 \pm 0.6c
Walking	7.6 \pm 1.4ab	8.4 \pm 0.7a	5.0 \pm 0.4b
Flying	2.6 \pm 0.4a	1.9 \pm 0.2a	1.0 \pm 0.1b
Mean total time (sec)	184.7 \pm 15.5a	228.6 \pm 11.9b	293.1 \pm 1.9c

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Table 2. Effect of plant damage on parasitization levels of FAW larvae by A. marginiventris.

	Type of plant damage		
	None	Artificial	FAW
% larvae collected:			
Off plant (A)	5.1±0.9a	18.1±0.5b	41.8±2.7c
On leaves (B)	74.4±1.8a	61.1±3.0b	45.5±2.8c
Within whorl (C)	20.5±2.2a	20.9±2.6a	12.8±1.4b
% larvae parasitized:			
In (A)	100.0a	100.0a	100.0a
In (B)	2.2±1.3a	5.7±2.2a	5.7±1.9a
In (C)	0a	0a	0a
Total % parasitization	7.0±1.1a	21.7±2.5b	44.4±2.3c
% superparasitization	0a	24.6±3.2b	25.3±3.5b

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Fig. 5. Attraction of A. marginiventris females to different types of corn plant damage (FAW larvae present).

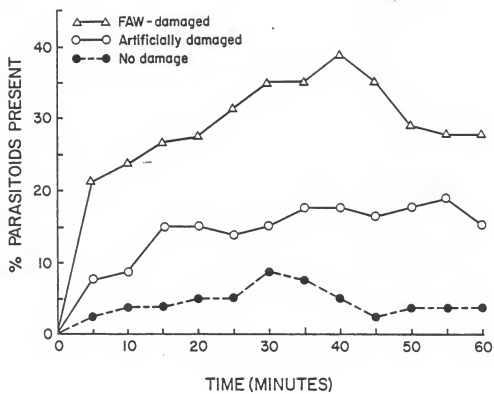
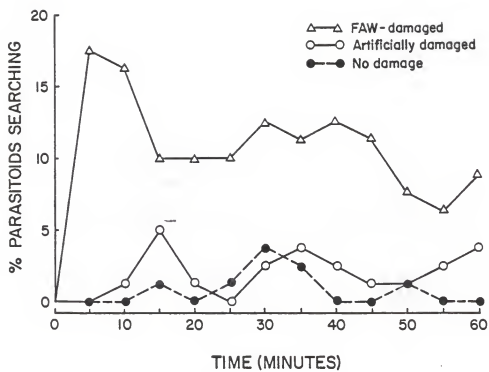


Fig. 6. Effect of different types of corn plant damage on searching by A. marginiventris females (FAW larvae present).



Thus plant damage, whether artificially or host-inflicted, plays an important role (although not equally) in attracting and stimulating A. marginiventris. Many workers have reported similar influences of plant damage or plant odors (Arthur 1962, Monteith 1964, Read et al. 1970, Camors and Payne 1973, and Nettles 1979). However, there is also infrequent documentation of failure to find any plant effects (Esmaili and Wilde 1971, McKinney and Pass 1977). It is reasonable to believe that in most cases, plants have an important influence on the foraging behavior of parasitoids. Vinson (1977) has pointed out that the plant often provides the first cues in the chain of events that leads to host location. Price et al. (1980) have also stated that a closer look at insect/plant interactions often reveals that plants have many effects not only on phytophages but also on the natural enemies of these phytophages. In fact, the entomophage can be considered as part of the plant's battery of defenses against phytophages. In nature, then, the evolution of some kind of mutualistic relationship between natural enemies and the plant of their host is highly probable and this could involve semiochemicals which Nordlund and Lewis (1976) have proposed to call "synomones".

Further support of the important role of plants is given by the work of Hendry et al. (1976a,b). They showed that the primary food sources (corn and potato) of two host insects (Heliothis zea (Boddie) and Phthorimaea operculella (Zeller)) contain significant concentrations of the chemicals (tricosane and heptanoic acid) that serve as host-seeking stimulants for their parasitoids (Trichogramma evanescens Westwood and Orgilus lepidus Muesebeck). It is very possible that kairomones involved in host-seeking originate in plants in addition to de novo synthesis in the insects.

Damaged plants may be giving off such chemicals which are then perceived by parasitoids.

Once parasitoids are attracted to the plant, they are affected by another level of chemical stimuli acting as arrestant and search stimulants. The result of the temporal modifications of behavioral activities and parasitization of host larvae on differentially damaged corn plants support this conclusion.

SECTION II
BIOLOGICAL AND BEHAVIORAL STUDIES ON THE
RESPONSE OF APANTELES MARGINIVENTRIS
(CRESSON) TO ITS HOST'S KAIROMONES

Introduction

Research on kairomones has gained momentum over the years as the prospects of using these semiochemicals for beneficial behavioral manipulation of parasitoids continue to grow. Of great importance to the study of these chemicals is the development of a reliable and specific bioassay. The type of bioassay conducted depends on the nature of the behavior under investigation. In general, 2 kinds of bioassay set-ups have been used, namely, (1) an olfactometer for those compounds that attract the parasitoid from a distance greater than several centimeters and (2) an arena type set-up for short-range chemicals (Vinson 1977). Many of the kairomones studied and isolated to date are of low volatility and only elicit responses over extremely short distances. Quednau (1967) and Vinson (1968) called these contact chemicals. Test parasitoids respond to these contact chemicals by antennation (Vinson and Lewis 1965, Lewis and Jones 1971) and/or ovipositor probing (Hendry et al. 1973, Vinson 1975a, Vinson et al. 1976, Henson et al. 1977) after antennal, tarsal or ovipositor contact have occurred. Thus, a small arena in which the parasitoid is comfortably confined, allowed to come into direct contact with the test substrate, and easily observed appears to be most appropriate. Whether the arena is a small vial, large bottle or a petri dish depends on the behavior

of the test insect as well as many other factors such as ease of handling and observation, disposability, turn-over efficiency, etc. For many hymenopterous parasitoids, the petri dish with the test substance applied as a spot on a filter paper appears to work well.

In addition to the consideration placed on the kind of bioassay set-up to be used, several behavioral and biological factors pertaining to the test parasitoids and source of kairomones are also important. For example, the parasitoid female may have a premating and/or preovipositional period in which it fails to respond to hosts. It has also been shown that response to hosts is a matter of experience in some parasitoids (Vinson 1977). Parasitoids have been observed to fluctuate in their response to host kairomones during different times of the day. Weseloh (1980) observed Apanteles melanoscelus (Ratzeburg) examining gypsy moth silk more intensely in the afternoon. The antennae of parasitoids are important chemosensory organs for the perception of kairomones in many parasitoids. Parasitoids with defective or damaged antennae may affect the outcome of bioassays. The procurement of kairomonal samples from hosts for study is often difficult because of the small size of the host stage attacked. Thus, to facilitate the collection of substantial amounts of host substances for research, it is relevant to check out the possibility of using samples from larger instars of the host larvae. Since no two parasitoid/host systems are exactly the same in all aspects, it is of importance that each be individually investigated so as to develop or adopt the most suitable bioassay. In the following series of studies, several important biological and behavioral aspects pertaining to the behavioral response of Apanteles marginiventris (Cresson) to its host's kairomones were investigated so that a reliable bioassay

could be adopted.

Methods and Materials

Rearing Experimental Insects and Planting of Corn

FAW and the parasitoids were reared and corn plants grown as previously described.

Evaluation of Bioassay Arenas

Two types of arenas were investigated, viz. vials and petri dishes. Vials tested were of 3 sizes, 1 dram, 2 drams and 4 drams. Petri dishes were of 5 cm, 10 cm and 15 cm diameters. For the vial bioassay, the female parasitoid was captured within a plexiglass holding cage using the vial itself. The test substance was administered by spotting it on a strip of filter paper which was then inserted into the vial. The thumb, held over the opening of the vial, acted as a cap as well as a clamp for the strip of filter paper. For the petri dish arena, the test substance was spotted onto the center of a piece of No. 1 Whatman filter paper. The female parasitoid was caught with a gelatin capsule from the holding cage and transferred into the petri dish which was subsequently closed with its own cover. Parasitoids were allowed to acclimatize and were then observed for 60 seconds under two 20-watt fluorescent bulbs under ambient laboratory conditions (26°C, 50% RH and normally lighted). The behavioral pattern of the parasitoid with and without test substance (piece of FAW-damaged corn leaf) was observed and traced by means of a grease pencil. The criteria used to evaluate the arenas were the ease of transferring the parasitoid into the arena, general behavior of the parasitoid when confined, ease of administering the test substance, the ease of manipulating the parasitoid.

toid over the spot of test substance (if necessary), time required for releasing tested parasitoids, and the general efficiency and frequency with which the assays could be run.

Experienced and Inexperienced Parasitoids

Sixty female parasitoids of uniform age (3-day old) were obtained from the principal holding cage. These were divided into 3 equal groups. Group A was not exposed to any host material, Group B was exposed to FAW-damaged corn leaves without larvae and Group C was exposed to damaged corn leaves with second instar larvae present. Exposure lasted 30 minutes. All groups were held separately in plexiglass cages and used for bioassay 1 hour later. Response to FAW-damaged corn leaf was scored on a 4-point system developed by Lewis and Jones (1971). A score of 3 equals intense response (antennal palpation and/or ovipositor probing) when contacting the 'kairomone patch' on the first pass. Response on the second and third passes was scored 2 and 1 respectively. A score of 0 was given when no response was elicited after 3 passes. The number of visits within 60 seconds of actual observation and the duration of the first visit were recorded. A new petri dish set-up was used for every 4 parasitoids.

Virgin and Mated Females

Unclosed 3-day old parasitoid cocoons were harvested from sting units. Seventy-five cocoons were put aside in a plexiglass cage supplied with honey and water for adult eclosion and subsequent mating. Another 75 cocoons were individually put in 1 ounce plastic cups. A hole was punched in the cover of the plastic cup and a small plug of cotton inserted. The cotton plug was saturated daily with a 50:50

honey/water solution. Additional male parasitoids were added to the plexiglass cage as eclosion occurred to ensure successful mating. Both the parasitoids in the plexiglass cage and the 1 ounce cups were examined daily to check for females. When 15 (or more) females from each group eclosed on a particular day, these 2 groups of 15 females were used for subsequent bioassay. The response of each group (mated and virgin females) to FAW-damaged corn leaf was bioassayed daily for a period of about 1 week.

Diel Activity

The response of 2 to 4-day old mated and experienced female parasitoids at different times of the day was studied using the FAW-damaged corn leaf/petri dish bioassay. Twelve parasitoids were bioassayed each time. The times studied were 0800-0830 h, 1000-1030 h, 1200-1230 h, 1400-1430 h, 1600-1630 h and 1800-1830 h.

Antennectomy Effects

Female parasitoids (2 to 4-day old) were anaesthetized with CO₂ and their antennae were clipped under a binocular microscope. The treatments studied were no antennectomy, 1 antenna removed, half of both antennae removed and both antennae completely removed. Fifteen parasitoids were used for each treatment and treated groups were kept separately. At least 3 hours of recuperation were allowed after antennal removal. The response of parasitoids to FAW-damaged corn leaf was bioassayed as before.

Response to Kairomones of Different FAW Instars

Sections of corn leaves damaged by FAW larvae of various instars were evaluated to determine if the leaves would elicit antennation and

ovipositor probing in 2 to 4-day old parasitoids. The corn leaf sections were of uniform size (1x1.5 cm) and had traces of frass on them. The responses of 20 female parasitoids were scored in a petri dish bioassay.

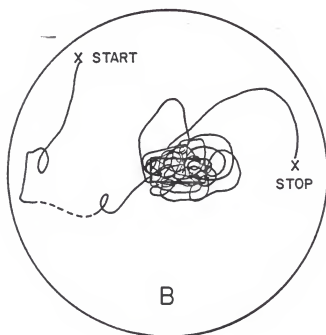
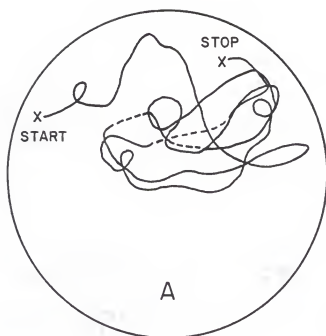
Effect of Larval Age on Parasitization

Six ages of FAW larvae were studied. These were newly-hatched (less than 12 h), 24 h, 48 h, 72 h, 96 h and 120 h old larvae. For each age group, 4 replicates were set up and each replicate consisted of 30 larvae placed on diet cubes (2 cm^3) in a sting unit (plastic cup 7.5 cm x 10 cm diam). A two-day old female parasitoid was introduced into each sting unit and allowed to remain there for 24 hours. At the end of this exposure period, larvae were individually transferred and reared separately in 1 oz. plastic cups. The rearing cups were kept in a controlled environment cabinet maintained at 27°C and 70% RH and illuminated with two 20-watt fluorescent bulbs set on a 14 h photophase. Records were kept for parasitoid larval duration, % parasitization, % eclosion from cocoons and % multiple parasitoid development within a single host.

Results and Discussion

Petri dishes as a group were better than vials as bioassay arenas. It was easier to prepare and present test samples to parasitoids in petri dishes. The movement of the parasitoid was more easily observed in petri dishes. Ten cm petri dishes were favorable in all aspects evaluated. Fig. 7 shows differing patterns of the behavior of female A. marginiventris held in petri dishes with and without the presence of a piece of FAW-damaged corn leaf. When contacting the corn leaf

Fig. 7. Behavioral pattern of A. marginiventris held in a 10 cm petri dish with and without a FAW-damaged section of corn leaf.



("kairomone patch"), the parasitoid exhibited intense antennal palpation, ovipositor probing and klinokinesis. It often moved away from the "kairomone patch", underwent klinotactic responses which directed it back to the patch. This behavioral pattern is typical of a parasitoid's response to kairomones presented in a petri dish bioassay arena.

Table 3 shows the results of the response of inexperienced (no host exposure) and experienced (exposed to host and/or host damage) parasitoids to kairomones. There was no significant difference in the scoring of the 3 types of parasitoid females. However, a significantly higher proportion of inexperienced females made multiple visits to the kairomone patch as compared to both categories of experienced females. The mean duration of the parasitoid's first contact with the kairomone patch was significantly shorter for inexperienced females. It is possible that inexperienced parasitoids made use of their short first contact with the kairomonal patch as a "learning" situation and subsequently made repeated visits. Since the bioassay essentially evaluates the response of the parasitoid to host kairomones acting as releasers or sign stimuli, fixed-action patterns should be evoked from both inexperienced and experienced parasitoids, especially when such parasitoids are drawn from a genetically homogeneous laboratory population that has undergone many generations of inbreeding. It appears that the use of inexperienced or experienced parasitoids in this case is not critical. However, experienced parasitoids are still preferred in most cases especially when samples bioassayed are less "holistic" as sources of kairomones, when compared with FAW-damaged corn leaf sections.

Table 3. Response of experienced and inexperienced *A. marginiventris* to FAW-damaged corn leaf section.

	Type of parasitoid		
	Inexperienced	Experienced (has oviposited)	Experienced (has not oviposited)
Mean response	3.0±0.2a	2.9±0.3a	3.0±0a
% responding strongly	95.0	90.0	100.0
% probing with ovipositor	100.0	95.0	100.0
% making multiple visits	70.0a	36.0b	20.0b
Mean duration of 1st visit (sec)	34.8±20.6a	56.5±4.5b	58.8±2.5b
Mean number of visits	2.2±0.9a	1.3±0.6b	1.3±0.4b

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

The reactions of virgin and mated A. marginiventris females to kairomones showed substantial differences in patterns. Mated females ranging in age from 1 to 3 days exhibited a more intense bioassay response (Fig. 8), had a higher percentage of females responding (Fig. 9) and displayed a greater propensity to probe with their ovipositors (Fig. 10). Similar bioassay results occurred for 4 to 5-day old mated and virgin females. Commencing on day 6 and continuing through day 8, virgin females declined more rapidly in all 3 bioassay responses than did mated females. In general, 2 to 4-day old mated females appeared to be most responsive as a group. These results closely parallel the observations of Kunnalaca and Mueller (1979) in which A. marginiventris parasitizing Plathypena scabra (F.) were reported to be most active on the 2nd and 3rd days. Longevity of adult A. marginiventris females is ca. 7-10 days under laboratory conditions. It is reasonable that 2 to 4-day old females are observed to be most responsive while older ones decline in responsiveness. With increasing age, there is a deterioration in physical condition, and resorption of oocytes in many insects (Chapman 1971). These may be the causes of a decline in responsiveness of older parasitoids.

Mating appears to influence the response of females in some way. This is contrary to the report by Douthett et al. (1976) that newly-emerged female parasitoids, irrespective of mating, are generally well-equipped for their special role of finding hosts in the environment. Mating perhaps brings about an earlier on-set of the appetitive behavior of the parasitoid while virgin females may still retain the urge to satisfy their mating needs before seeking out hosts for oviposition. However, at some point, the pressure of maturing oocytes may override

Fig. 8. Age-related response of virgin and mated A. marginiventris females to FAW-damaged corn leaf sections.

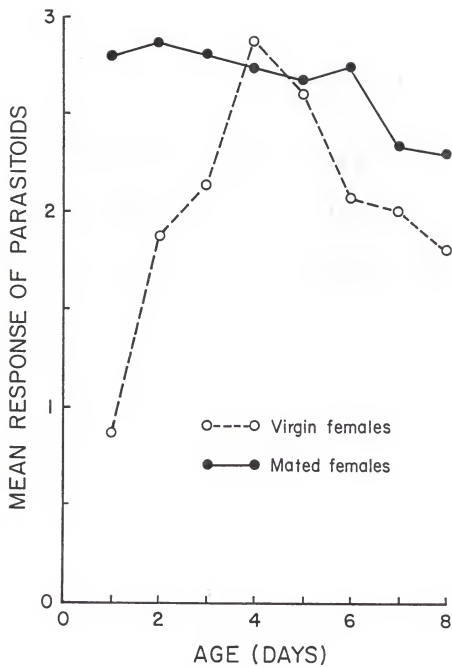


Fig. 9. Percent virgin and mated A. marginiventris females responding strongly to FAW-damaged corn leaf sections.

Note: A strong response = a response score of 3.

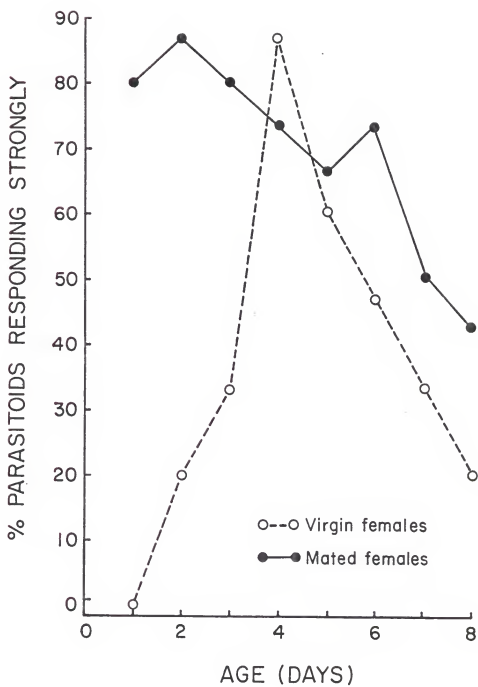
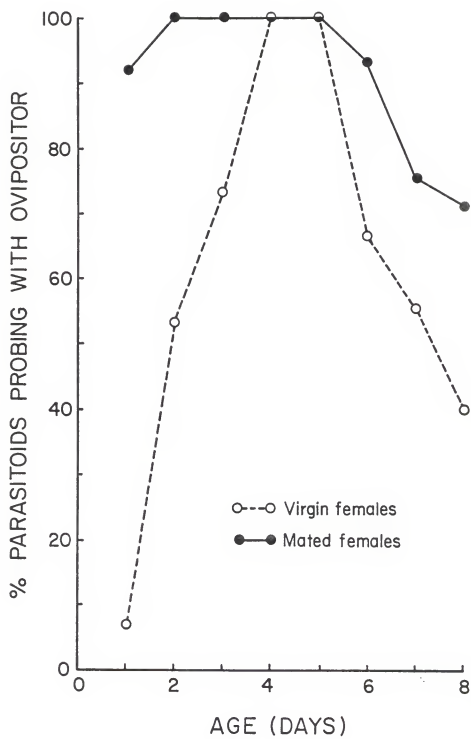


Fig. 10. Percent virgin and mated A. marginiventris females exhibiting ovipositor probing in response to FAW-damaged corn leaf sections.



their urge to be mated and they may then become responsive to seek out hosts for the purpose of oviposition as seen in 4-day old virgin females. For the purpose of reliable bioassays, mated 2 to 4-day old females appear to be most suitable.

Evaluation of the response of A. marginiventris to kairomones at 6 different times throughout the photophase showed no significant differences in response between the hours of 0800 and 1800 (Table 4). Parasitoids appear to be most active in the afternoon around 1400 hours. A. marginiventris is a day-adapted species and has been observed searching for hosts in bright sunlight in open corn fields (Ashley, personal communication). This is generally true for many parasitoids (Vinson 1975a, Kunnalaca and Mueller 1979, Weseloh 1980). Conducting bioassays with A. marginiventris during the photophase hours, then, poses no problem.

The degree of antennectomy had a significant effect on the response of A. marginiventris to host kairomones (Table 5). Parasitoids with 1 antenna completely removed were affected primarily in their ability to respond strongly. Clipping off the terminal 8 of the 16 flagellomeres on both antennae caused a significant reduction in all responses and no response was elicited from parasitoids with both antennae completely removed. Antennal amputation of insects often places them in a state of akinesis from which they are aroused only with difficulty (Dethier and Chadwick 1948). The importance of the antennae in host-seeking has been indicated by a number of authors (Weseloh 1971, Greany and Oatman 1971, Richerson et al. 1972). In addition, Norton and Vinson (1974) and Dmoch and Rutkowska-Ostrowska (1978) reported the presence of 'bent tip' receptors and sensory

Table 4. Diel response of A. marginiventris to FAW-damaged corn leaf sections.

	Time of day					
	0800	1000	1200	1400	1600	1800
Mean response	2.9±0.3a	2.9±0.3a	2.9±0.3a	3.0±0a	2.9±0.3a	2.8±0.4a
% responding	100	100	100	100	100	100
% responding strongly	91.7	91.7	91.7	100	91.7	75.0
% probing with ovipositor	91.7	100	100	100	91.7	91.7

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

¹ All tests were conducted within a half hour period after the indicated time.

Table 5. Effect of antennectomy on the response of A. marginiventris to FAW-damaged corn leaf section.

	Degree of antennectomy			
	None	1 antenna removed	½ of both removed	Both antennae removed
Mean response	2.9±0.3a	2.7±0.4a	1.3±0.6b	0c
% responding	100	100	93.3	0
% responding strongly	93.3	73.3	0	0
% probing with ovipositor	100	100	26.7	0

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

bouquets of sensillae on Cardiochiles nigriceps Viereck (a braconid) and Trichomalus perfectus Walker (pteromalid) in the terminal antennal segment. It is possible that the terminal portion of the antennae of A. marginiventris has the same kind of sensory receptors present. This would certainly explain why cutting off the apical antennal segments caused a significant reduction in the parasitoid's ability to respond. The conclusion drawn from this experiment is that parasitoids with damaged or defective antennae should not be used in bioassays.

A. marginiventris females did not exhibit a preference for corn leaves damaged by a particular FAW instar (Table 6). Parasitoids responded strongly and equally to all test samples. This indicated that there was no difference, essentially, between kairomones of the various host instars produced in association with corn leaves. Therefore, larger and more easily handled FAW instars could be used in acquiring appreciable quantities of those substances for testing as sources of kairomones.

The results of parasitization of different ages of FAW larvae are shown in Table 7. Parasitization was highest in 48 h old larvae. This was also shown to be the case for A. marginiventris parasitizing Trichoplusia ni (Hubner) (Boling and Pitre 1970). However, the situation in the field may be different. Vickery (1929) reported that first instars are preferred and may be stung before they dispersed from the egg mass. In general, 24 to 96 h larvae (3rd instar) were heavily parasitized. Larvae older than 120 h were not as successfully parasitized. This could be due to the ability of the older and larger hosts to physically defend themselves, encapsulation of the developing parasitoid or the fact that the cuticle of older larvae was too thick for successful stinging and

Table 6. Response of A. marginiventris to corn leaves damaged by different FAW instars.

	FAW instar					
	I	II	III	IV	V	VI
Mean response (\pm SE)	2.90 \pm 0.30a	2.95 \pm 0.22a	3.0 \pm 0a	2.95 \pm 0.22a	2.95 \pm 0.22a	3.0 \pm 0a
% responding	100	100	100	100	100	100
% responding strongly	90.0	95.0	100	95.0	95.0	100
% probing with ovipositor	95.0	95.0	100	100	95.0	100

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Table 7. Effect of host age on parasitization and larval development in *A. marginiventris*.

	Age of FAW instar					
	12 h	24 h	48 h	72 h	96 h	120 h
Mean larval duration (days)	7.7±0.1a	7.2±0.3a	6.9±0.3a	7.0±0a	6.8±0.2a	7.9±0.1a
% parasitization	53.8±18.7a	79.1±14.3b	94.1±4.2c	81.7±12.9b	70.8±5.2b	45.0±11.8a
% parasitoid eclosed	81.0±13.5a	95.3±4.1a	94.8±3.4a	93.6±8.5a	94.1±1.9a	90.3±2.9a
% multiple cocoon	1.3	0	1.9	0	0	12.7

Means in the same row followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

oviposition. The first reason appears to be valid up to the early stage of the fifth instar as immobilization of these larvae yielded some cases of successful oviposition by the parasitoid (Loke, unpublished data). The results of the above parasitization studies in conjunction with those of the previous experiment support the conclusion that different host ages or instars are suitable as sources for the procurement of kairomones.

SECTION III
SOURCES OF FAW KAIROMONES WHICH ELICIT A
HOST-SEEKING RESPONSE IN APANTELES MARGINIVENTRIS (CRESSON)

Introduction

One of the most interesting aspects of insect parasitoid behavior is the means by which parasitoids find their host. Thorpe and Jones (1937) and Laing (1937) were among the first workers to observe that host odor was a factor in the host-finding of such parasitoids. Since then, various investigators (Vinson and Lewis 1965, Vinson 1968, Lewis and Jones 1971, Hendry et al. 1973, Jones et al. 1973, Weseloh 1974, Leonard et al. 1975, Vinson 1977, Longhurst and Baker 1981) have found that parasitoids often respond to host indicators such as frass, salivary secretion, cuticle odor, silk and moth scales and that these indicators contain chemicals which act as primary stimuli for host-finding by the parasitoids. Chemicals of this kind are called kairomones (Brown et al. 1970, Whittaker and Feeny 1971, Nordlund and Lewis 1976) and are defined as transspecific chemical messengers produced by one species that induce a behavioral or physiological response in another species wherein the latter species or recipient is favored. It has also been shown that such chemicals are fairly varied in nature and can be present in more than one location in the host insect (Lewis et al. 1976a, Vinson 1977). More than 10 kairomones mediating host-finding and host acceptance of several parasitoid/host relationships have been identified and it has also been shown that these chemicals

are potentially useful for parasitoid management and have not been found to be harmful to other biota in the environment (Lewis et al. 1976a, Vinson 1977).

In a previous study, the host-finding behavior of Apanteles marginiventris (Cresson) has been described and it was shown that this parasitoid is attracted and stimulated by plant/host factors to locate its host, the fall armyworm. Various steps in the "find and attack" cycle were observed to be influenced by searching stimulants. In the present study, host substances and corn leaves are examined as possible sources of host-seeking cues that elicit a response in A. marginiventris.

Methods and Materials

Rearing Experimental Insects and Growing Host Plants

Fall armyworm, Spodoptera frugiperda (J. E. Smith), and A. marginiventris were reared as before. Plants (corn, soybean, Bermuda grass, peanut, cowpea) were grown in the greenhouse in 15 cm diam and 14.5 cm high plastic planter pots.

Sources of Kairomones from Corn-Reared FAW

Frass, cuticle odor, exuviae, silk, oral secretion, hemolymph and scales were examined as possible sources of kairomones for A. marginiventris. Materials were obtained from corn-reared second or third instar larvae, female pupae and adult females, and applied as a spot onto a 9 cm Whatman No. 1 filter paper for bioassay in a 10 x 1.5 cm plastic petri dish. Frass (0.5 mg), ca. 10 ul of oral secretion (obtained by holding the larva behind the head and at the tail end, and gently forcing it to orally secrete onto the filter paper), ca. 10 ul of hemolymph (obtained by pin-pricking the larva), 25 rolls of silk

around a minuten pin, 5 transfers of larval cuticle odor (a single transfer consisted of rubbing fifth/sixth instar larvae onto the filter paper), a complete piece of exuviae, 5 transfers of pupal cuticle and some scales from the wing of a female moth were used. Thirty 2 to 4-day old, mated and experienced A. marginiventris females were bioassayed and their responses scored on a 4-point system. Fresh set-ups were used for each female tested. Bioassays were conducted under ambient laboratory conditions and beneath (ca. 30 cm away) two 20-watt fluorescent bulbs as previously described.

Response to Frass from Larvae Reared on Different Food Sources

Frass was obtained from FAW larvae reared on diet, FAW larvae, corn, bermuda grass, peanut, cowpea and soybean leaves. Each type of frass (0.5 mg) was bioassayed using 30 mated and inexperienced (previously not exposed to host-damaged corn leaves) 2 to 4-day old female A. marginiventris. Bioassays were conducted as previously described.

Response to Corn Leaf and Corn Leaf/Host Substance Combinations

Bioassays were carried out to examine the response of 2 to 4-day old, mated and experienced female A. marginiventris to different forms of corn leaf damage and combinations of corn leaf/host substance. Frass (0.5 mg) from corn-reared FAW larvae was used as a standard. The various forms of corn leaves investigated were intact corn leaf (cut edge was taped), corn leaf with cut edges exposed, corn leaf stipled with a pin to simulate feeding damage, crushed corn leaf (0.5 mg) and corn leaf juice (10 ul). The corn leaves were sectioned into 1x2 cm pieces for the bioassays. Combinations of corn leaf/host substances (diet-reared FAW) consisted of stipled corn leaf and oral secretion,

stipled corn leaf and frass, stipled corn leaf and cuticle odor, and stipled corn leaf plus oral secretion, frass, and cuticle odor. Twenty parasitoid females were bioassayed as previously described.

Extraction of Kairomones

Frass from corn-reared FAW larvae was collected and kept frozen (ca. -10°C) in tightly capped glass vials until a sufficient amount had accumulated. Frass (500 mg) was extracted with 10 ml of each solvent. The solvents used were deionized/distilled water, nanograde methanol, chloroform and n-hexane. Extraction consisted of grinding the frass in the solvent with a mortar and pestle for about 3 minutes. The extract was then filtered through a Whatman No. 1 filter paper and used immediately for bioassays. Bioassays were conducted by spotting 5 μl of extract onto the filter paper and allowing sufficient time for the solvent to evaporate before placing the filter paper into the petri dish. Excess extracts (except the water extract which was stored in the regular refrigerator compartment) were stored at ca. -10°C in tightly stoppered vials. Equivalent amounts of corn leaf were similarly extracted and bioassayed. Extracts of scales were made by soaking 5 female adults with 10 ml of each solvent for 60 minutes followed by filtration. Twenty 2 to 4-day old, mated and experienced parasitoids were bioassayed. Frass (0.25 mg) was used as a standard.

Results and Discussion

The results of bioassaying 8 different host substances as potential sources of kairomones in A. marginiventris females are shown in Table 8. Positive responses occurred for all substances tested. Since the amount of each host substance used in the bioassay was arbitrarily assigned, it

Table 8. Response of *A. marginiventris* to substances derived from corn-reared FAW.

FAW substances	Mean response (\pm SE)	Percent		
		responding	responding strongly	probing with ovipositor
Frass	3.00 \pm 0a	100	100	100
Larval cuticle odor	2.87 \pm 0.06ab	100	86.7	43.3
Pupal cuticle odor	2.83 \pm 0.07ab	100	83.3	33.3
Scales	2.83 \pm 0.07ab	100	80.0	90.0
Exuviae	2.80 \pm 0.07ab	100	80.0	70.0
Silk	2.67 \pm 0.11b	100	70.0	46.7
Oral secretion	2.63 \pm 0.11b	100	70.0	53.3
Hemolymph	1.26 \pm 0.14c	83.3	3.3	3.3

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

may not be completely valid to make statistical comparisons of the relative stimulatory effects of these substances. Nevertheless, a statistical analysis of the data indicated that frass, larval cuticle odor, pupal cuticle odor, exuviae and scales were the most stimulating. Frass and scales induced the parasitoids to probe with their ovipositors more frequently. Oral secretion from starved, diet-reared, 5th instar fall armyworm larvae was also tested. The mean response (2.2) to this was lower than that for oral secretion from corn-reared larvae. This difference could be attributable to larval diet. Parasitoids showed no response to plain diet presented as bioassay samples. Response (attraction and stimulation to search) of parasitoids to the corn plant per se has already been demonstrated in an earlier study. Thus, it seems that oral secretions (salivary in nature) are stimulatory by themselves but elicited a stronger response when contaminated with slight quantities of regurgitated corn leaves. Silk extruded by the larvae may be contaminated with salivary secretions. Hence, its activity could be due to contamination, but on the other hand, it is also possible that host-seeking chemical(s) are present in the silk per se. Hemolymph, though eliciting response from a high % of the parasitoids tested, was the least stimulatory substance.

Larval cuticle odor, pupal cuticle odor, scales and exuviae were highly stimulating and no significant differences were found in the responses of parasitoids to them. These four substances are of similar structural origin, thus their biochemical composition may be also similar. The source of larval and pupal cuticle odor was actually the epicuticle layer since samples for bioassays were prepared by rubbing the larva or pupa on filter paper. Therefore, the chemical substance

actually transferred onto the filter paper probably was derived from the wax and cement layer of the epicuticle. This layer contains many kinds of lipids and it has been shown for several insect species that long-chain hydrocarbons are a major component of these lipids (Richards 1978, Baker and Nelson 1981). Long-chain hydrocarbons (tricosane, 13-methylhentriacontane, mixture of methyl esters of hentria, dotria and tritriacontanes) have been identified as important kairomones for parasitoid/host systems (Jones et al. 1971, Vinson et al. 1975, Jones et al. 1973) and many more have been implicated in other systems (Quednau and Hubsh 1964, Weseloh 1974, Schmidt 1974, Wilson et al. 1974, Leonard et al. 1975).

Long-chain hydrocarbons are fairly ubiquitous in insects. In addition to being present in cuticular tissues, these organic compounds have also been reported to be present in other substances such as hemolymph and oral secretions (Lewis et al. 1976a). Their presence in hemolymph, particularly in Lepidoptera, may be due to the presence of oenocytes in fat bodies and within the basement membrane separating the cuticle and the hemocoel. Oenocytes are known to produce hydrocarbons and lipoproteins for incorporation as the wax of the epicuticle (Chapman 1971). Hydrocarbons in salivary glands are believed to act as lubricants (Lewis et al. 1976a). The detection and known presence of hydrocarbons in so many kinds of host substances in general, and the fact that A. marginiventris responds positively to such host substances provide some reason to suspect that the kairomone(s) (host-derived) A. marginiventris is responding to may be some kind of hydrocarbon or related organic compound.

It is also interesting to note the kairomonal activity of pupal cuticle and moth scales, since A. marginiventris is strictly a larval

parasitoid. The possibility exists that kairomones present in larval cuticle are also found in pupal cuticle and moth scales or possibly A. marginiventris may be able to respond to a range of related chemicals if the kairomones from pupal cuticle and moth scales are biochemically different from those found in larval cuticle. The stimulatory effect of moth scales in nature is perhaps to be expected as A. marginiventris has been observed to attack newly-hatched host larvae before they have dispersed from the egg mass. Newly-hatched FAW larvae often do not feed on foliage until they have dispersed. Thus, parasitoids cueing in on these larvae do not have available cues emanated from host-inflicted damage. It is possible then for parasitoids to use moth scales, silk and/or oral secretions from the newly-hatched larvae as host-seeking cues.

The strong overall kairomonal activity of frass perhaps best epitomizes the research results. Frass contains exogenous and endogenous materials such as corn leaves and exuviae, and salivary secretions and intima. Frass appears, then, to contain all levels of chemical cues needed to elicit intense host-seeking responses. This is reflected by the results in Table 8 which shows that frass was highest in terms of scores registered, % parasitoids responding and % parasitoids probing with ovipositor.

The results reported regarding sources of kairomones eliciting a host-seeking response in A. marginiventris are consistent with findings reported by Jones et al. (1976), Lewis et al. (1976a,b), Vinson (1977), Sato (1979) and Longhurst and Baker (1981) for other host/parasitoid situations in which a variety of substances have been shown to be kairomone sources. That sources of kairomones can be diverse and varied

and yet have some common chemical link appears to be quite universal.

The results of testing corn leaves and corn leaf/host substance combinations as sources of host-seeking cues showed that corn leaves per se have some positive activity while stipled and crushed leaves elicited higher responses from the parasitoids (Table 9). Artificial plant damage has been shown to be attractive and stimulating to parasitoids and these results further confirm this finding. Parasitoids favored the untaped cut edges of the corn leaves, and reacted to stipled and crushed corn leaves much as they would to FAW-damaged corn leaves and frass. Stipled corn leaf and crushed corn leaf are mimics of real situations, and the behavioral response of the parasitoids to them indicates response to both physical cues and chemical ones. Findings reported by Hendry et al. (1976) have shown that the host plants of 2 insects contained substantial quantities of chemicals used as host-seeking stimulants by their respective parasitoids. It appears the same may be true in this study.

The high responses elicited by combinations of stipled corn leaves and host substances were expected. Combining plant and host-related factors creates a condition in which a series or hierarchy of host-seeking cues are available to the parasitoids and the intense responses elicited are, therefore, natural. It is also possible that some synergism or potentiation occurred when stipled corn leaves and diet-reared host substances were combined and presented as bioassay samples. This kind of situation has been reported by Sauls et al. (1979) for the response of Microplitis croceipes (Cresson) to a combination of homogenized cowpea cotyledons and frass of diet-reared Heliothis zea (Boddie).

Table 9. Response of *A. marginiventris* to corn leaves and combinations of stipled corn leaves and substances from diet-reared *FAW*.

Samples bioassayed	Mean response (\pm SE)	Percent		
		responding	responding strongly	probing with ovipositor
Lab. diet	0	0	0	0
Intact leaf	0.05 \pm 0.05a	5.0	0	0
Cut leaf	1.25 \pm 0.10b	100	0	5.0
Leaf juice	1.80 \pm 0.16c	100	15.0	0
Stipled leaf (SL)	2.15 \pm 0.17d	100	35.0	30.0
Crushed leaf	2.80 \pm 0.09e	100	80.0	70.0
SL + oral secretion (OS)	2.90 \pm 0.07e	100	90.0	85.0
SL + frass (F)	2.90 \pm 0.07e	100	90.0	95.0
SL + cuticle odor (CO)	2.95 \pm 0.05e	100	95.0	100
SL + OS, F and CO	3.00 \pm 0e	100	100	100

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Generally, high responses were elicited from the parasitoids to all frass regardless of the FAW larval food source (Table 10). This is probably due to the presence of substances from salivary secretions, intima and consumed exuviae which may account for kairomones in the frass irrespective of the host diet. However, plant materials as a group produced frass that was slightly more stimulatory than that from a meridic, artificial laboratory diet. This situation may be due to the presence of natural host-seeking chemicals or their precursors in plants and the absence of these chemicals in the ingredients of the laboratory diet. Food of the host has been shown to significantly influence the kairomonal activity of frass (Sauls et al. 1979) but this does not appear to be the case for A. marginiventris. Perhaps this is attributable to the fact that A. marginiventris has been reported from many ecosystems (Boling and Pitre 1970, Nickle 1977, Ashley 1979, Mueller and Kunjalaca 1979) and is therefore able to respond not only to frass derived from corn plants but also to many other plants on which S. frugiperda and the parasitoid's other hosts are known to feed.

Hexane, chloroform and methanol extracts of frass elicited significantly greater responses from A. marginiventris than did a water extract (Table 11). No response was observed when solvents per se were tested. The most pronounced differences between the standard and the extracts was noted in the % of parasitoids probing with their ovipositors. Serial dilutions of these extracts resulted in a substantial decrease in parasitoid response (Fig. 11). The results in Table 11 and Fig. 11 indicate that hexane and chloroform are the best solvents. The chloroform extract of corn leaves was significantly better than

Table 10. Response of A. marginiventris to frass of FAW larvae reared on different food sources.

Food source	Mean response (\pm SE)	Percent		
		responding	responding strongly	probing with ovipositor
Cow pea	2.70 \pm 0.09a	100	70.0	83.3
Lab. diet	2.73 \pm 0.08ab	100	70.0	43.3
Bermuda grass	2.77 \pm 0.08abc	100	76.7	90.0
FAW	2.80 \pm 0.07abc	100	80.0	53.3
Soybean	2.83 \pm 0.07abc	100	80.0	90.0
Peanut	2.93 \pm 0.05bc	100	93.3	100
Corn	2.97 \pm 0.03bc	100	96.7	100

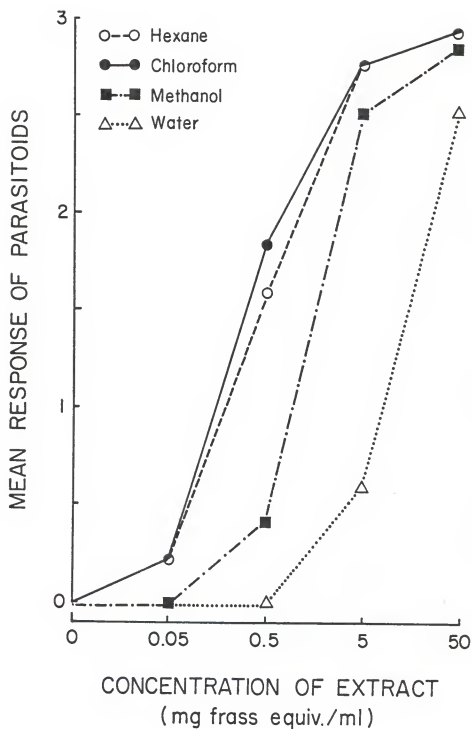
Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Table 11. Response of A. marginiventris to extracts of frass from corn-reared FAW larvae.

Material bioassayed	Mean response (±SE)	Percent		
		responding	responding strongly	probing with ovipositor
Standard:				
Frass (0.25 mg)	3.00±0a	100	100	100
Extracts:				
Hexane	2.90±0.06a	100	90.0	35.0
Chloroform	2.85±0.08a	100	85.0	35.0
Methanol	2.85±0.08a	100	85.0	25.0
Water	2.45±0.14b	100	50.0	15.0

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Fig. 11. Response of A. marginiventris females to serial dilutions of frass extracts from corn-reared FAW larvae.



the extracts of the other solvents (Table 12). The water extract was lowest in activity. These results seem to support the hypothesis that non-polar compounds are extracted and involved as kairomones for A. marginiventris. Moth scales were also extracted but the procedure used was not efficient and only slight kairomonal activity was observed for the hexane extract and none for the others.

Table 12. Response of A. marginiventris to extracts of corn leaves.

Extract	Mean response (\pm SE)	Percent		
		responding	responding strongly	probing with ovipositor
Water	0.95 \pm 0.20a	65.0	5.0	0
Hexane	1.45 \pm 0.20ab	85.0	10.0	5.0
Methanol	1.70 \pm 0.20b	90.0	15.0	5.0
Chloroform	2.60 \pm 0.11c	100	60.0	15.0

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

SECTION IV
POTENTIAL USES OF KAIROMONES FOR BEHAVIORAL
MANIPULATION OF APANTELES MARGINIVENTRIS (CRESSON)

Introduction

The potential for pest management by the behavioral modification of insects through the utilization of non-toxic agents was recognized by Wright (1965). Behavioral control of a pest may be brought about by chemical agents through inhibiting a correct response or eliciting an incorrect one. However, the manipulation or behavioral modification of natural enemies, such as insect parasitoids, requires a unique approach. Instead of attempting to elicit an incorrect response or inhibit a correct one, the ultimate goal of manipulation of entomophages is to redirect or stimulate a desired behavioral response. Semiochemicals, such as kairomones, involved in the host-finding of parasitoids and predators offer new concepts and potentially new methods for the regulation of pest populations via behavioral modification. Retention in the agroecosystem and orientation to host infestations by placing the parasitoids into the "find and attack" cycle are the primary objectives of chemical manipulation (Lewis et al. 1976b, Vinson 1977, Jones et al. 1978). Studies by Lewis et al. (1975a,b) have shown that the efficiency of released Trichogramma spp. as well as wild Trichogramma spp. was significantly improved by the application of the host-seeking stimulus, tricosane, in target areas. Though applied or endemic kairomones may positively improve parasitoid efficiency, the probability

of field-released parasitoids encountering these host-seeking stimuli is often very low. It has been commonly observed that parasitoids, upon release, may disperse into a new area before settling into a normal host-finding behavioral pattern. Gross et al. (1975) demonstrated that for released Trichogramma spp. and Microplitis croceipes, sign stimuli (releasers) such as moth scales, tricosane or larval frass could be effectively used to prestimulate these parasitoids so as to override their innate tendency to disperse and thereby improve performance resulting in significantly increased rates of parasitization over that of unstimulated parasitoids.

Apanteles marginiventris (Cresson) has been shown to respond to several host-seeking stimulants such as frass, cuticle odor, silk and scales of its host, the fall armyworm (previous section). The following series of experiments were conducted to evaluate whether the spraying of such host-seeking stimuli and stimulation of the parasitoids at the time of release could improve their performance and efficiency. A further potential use of kairomones was also investigated in which factitious hosts treated with FAW kairomonal extract were evaluated for their acceptance by A. marginiventris.

Methods and Materials

Rearing of Experimental Insects

FAW larvae and A. marginiventris were reared as described previously. Cabbage loopers and the velvet bean caterpillars were reared on a diet similar to that of the FAW. The wax moth larvae were reared on a modified pablum diet (Singh 1977).

Petri Dish Activation

The experimental universe consisted of a 15 x 2.5 cm petri dish. A 14 cm Whatman No. 1 filter paper was marked at 6 locations. Each location was equidistant laterally to the adjacent location and was situated radially 5 cm from the center point of the filter paper. Four kairomone treatment patterns were investigated. These were complete treatment, treated circles of 1 cm diam, 3 cm diam at the marked locations and no treatment (control). Rates of hexane frass extract application were equivalent in complete coverage and treated circles. At each location, an ecdysing second instar FAW larva which had been further immobilised by chilling was placed. A 2 to 4-day old, mated female A. marginiventris was introduced into the center of the petri dish and allowed to remain in the dish for 10 minutes. Time taken for the parasitoid to search and encounter a larva was recorded. Total time spent actively searching was also recorded. At the end of 10 minutes, the larvae were dissected to determine parasitization and super-parasitization rates. The experiment was repeated 10 times using a new female parasitoid each time. All experiments were carried out in ambient laboratory conditions under two 20-watt fluorescent bulbs.

Greenhouse Activation

Three rows of 3 corn seedlings each were planted in an aluminium foil cake pan (22x22x5 cm). Three spraying patterns of hexane frass extract were evaluated. The spraying patterns were no treatment (control), blanket treatment and spot treatment. Rates of application in blanket and spot treatments were equivalent. The blanket treatment was done by spraying evenly with a De Vibliss atomizer 163 for 30 sec (ca. 1.5 ml). Spot treatment was carried out by spraying equivalently

through a cardboard shield with five 3 cm holes cut out such that the holes were directly above the corn seedlings located in the 4 corners and center of the cake pan. Control pans were sprayed with hexane. Three second instar FAW larvae were placed onto each seedling after the sprayed plants had dried. Four 2 to 4-day old female parasitoids were released in the cake pan and observations of the released females were carried out for 10 minutes. Each cake pan was then carefully examined after 60 minutes and all FAW larvae were collected and dissected. Each treatment was replicated 6 times. Experiments were conducted between 1 and 3 p.m. Temperatures and humidity conditions were approximately 27°C and 70% RH.

Petri Dish Stimulation

An uncovered 15 cm petri dish was used as the experimental universe. Six locations were marked off as previously described. An ecdysing second instar FAW larva, previously chilled, was placed at each location. Some frass was spotted around each larva. The treatments consisted of smearing either hexane frass extract or fresh frass over the lip of the vials used for capturing experimental female parasitoids from a holding cage. A 0.25 dram shell vial was used to capture and transfer the parasitoid to the open petri dish. The uncapped vial was placed in the center of the petri dish and the parasitoid's behavior was observed for 10 minutes. At the end of the test period, larvae were dissected to determine parasitization. Five trials were conducted for each treatment. The experiment was repeated 5 times.

Greenhouse Stimulation

Corn seedlings were grown in cake pans as previously described. Three second instar FAW larvae were placed on each seedling and 4 female, 2 to 4-day old parasitoids were released from a 1 dram vial placed in the center of the cake pan. The lip of the vial was either treated with fresh frass, hexane frass extract, or not treated at all. The behavior of released female parasitoids was observed for 10 minutes. After 30 minutes, the cake pans were carefully examined and all FAW larvae collected for dissection to determine levels of parasitization. The experiment was repeated 5 times.

Kairomone Treatment of Natural and Factitious Hosts

The effect of treating highly acceptable (FAW), moderately acceptable (Trichoplusia ni, cabbage looper) and normally non-acceptable (Anticarsia gemmatilis, VBC and Galleria mellonella, greater wax moth) larvae with hexane frass extract was investigated. All larvae were reared on a pinto bean diet, except the wax moth. Chilled second instar larvae (third instar for the wax moth) were topically treated with 1 ul of extract. Treated larvae were put into 15 cm petri dish. A female A. marginiventris was introduced and all larvae were dissected after 30 minutes of exposure. The experiment was conducted under ambient laboratory conditions (ca. 27°C and 55% RH) and repeated 5 times.

Results and Discussion

The pattern of kairomonal extract significantly affected percent parasitization, time required for first host contact, and the amount of time spent searching (Table 13). The blanket treatment displayed

Table 13. Effect of pattern of kairomonal extract treatment on parasitization by A. marginiventris of FAW larvae in petri dishes.

Treatment	Percent		Mean time for first contact (min)	Mean overall search time (min)
	parasitization	superparasitization		
Control	25.0a	16.7a	3.47±0.15a	2.83±0.23a
1 cm spot	40.0b	23.3ab	2.27±0.16b	3.99±0.11b
3 cm spot	56.7c	33.3b	2.26±0.15b	4.83±0.15c
Blanket treatment	80.0d	25.0ab	0.86±0.05c	6.49±0.24d

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

the highest % parasitization, shortest time for first host contact and the greatest amount of searching time. The 2 spot treatments were generally intermediate between the control and blanket treatments. More hosts were parasitized and overall searching time was longer for the 3 cm spot treatment than for the 1 cm spot treatment. In the control treatment, parasitoids did not exhibit an intense searching behavior but instead remained for the majority of the time on the underside of the petri dish cover. Parasitoids in close proximity to kairomone spots or in actual contact with the treated filter paper displayed excitement and an intense searching behavior. The results obtained suggest that kairomones stimulated the parasitoids and activated a more effective searching pattern. Parasitoids in treated dishes searched extensively rather than remaining at one particular location. Thus, the kairomones were not acting as attractants. The results concurred with those reported by Lewis et al. (1975) for Trichogramma spp. The high % of superparasitization is probably an artifact of parasitoid confinement within a close arena and probably does not occur in field situations. Also, the difference between % superparasitization in the control treatment versus the other treatments supports the observations of higher activity and more effective searching by parasitoids activated by the kairomones present on the filter paper.

Results of the greenhouse experiment indicated that all 3 treatments were significantly different. Blanket sprayed pans had the highest % parasitoids retained and % parasitization of FAW larvae while spot treated pans were intermediate with the control treatment or untreated pans being the lowest (Table 14). The lower figures for % parasitization in these treatments as compared to the petri dish

Table 14. Effect of pattern of kairomonal extract spraying on parasitization by A. marginiventris of FAW larvae in pans of corn seedlings.

Treatment	% parasitoids retained	Percent	
		parasitization	superparasitization
Control	8.3a	1.9a	0
Spot sprayed	29.2b	13.8b	0
Blanket sprayed	50.0c	28.0c	0.6

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

experiment may be attributed to differences in experimental set-up and environmental conditions. Parasitoids used in the petri dishes were artificially confined but in the cake pan arrangement, released parasitoids could leave the corn seedlings. This was observed to be the case, especially in untreated pans. However, the overall trends in both experiments are parallel, that is, parasitoids released into kairomone treated arenas were stimulated and activated to search more effectively. The continual reinforcement of the host-seeking response in blanket treated pans was probably the reason for the resulting higher parasitization of FAW larvae. In untreated pans, parasitoids did not contact kairomones and most followed their innate tendency to disperse. Those which remained were only stimulated if their random movement resulted in contacting a host.

Stimulation of parasitoids with kairomone extract or frass at the time of release into the petri dish resulted in significantly higher % of parasitoids retained and searching as well as higher % of host larvae parasitized when compared to no stimulation (Table 15). Frass appeared to be a more effective stimulant than its hexane extract. This is probably because the frass represents an unaltered, more concentrated natural source of host-seeking stimuli. As discussed previously, frass probably contains all levels of chemical stimuli needed to elicit an intense host-finding response in A. marginiventris. Table 16 shows the results of a parallel experiment in the greenhouse. The differences in magnitude of the parameters observed are because of differing experimental designs. However, the trends were the same in both experiments. Significant differences were found between all treatments with highest % retention of parasitoids, % searching parasitoids and % parasitization

Table 15. Effect of prestimulation with kairomones on behavior of released A. marginiventris in the laboratory.

Treatment	Percent		
	retained	searching	parasitization
Control	24.0a	0a	0a
Extract stimulated	64.0b	60.0b	32.6b
Frass stimulated	76.0b	76.0b	34.8b

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

Table 16. Effect of prestimulation with kairomones on behavior of released A. marginiventris in the greenhouse.

Treatment	Percent		
	retained	searching	parasitization
Control	10.0a	5.0a	1.5a
Extract stimulated	35.0b	35.0b	9.6b
Frass stimulated	65.0c	65.0c	15.5c

Means in the same column followed by the same letter are not significantly different (5% level) as determined by Duncan's multiple range test.

of FAW larvae recorded from frass-stimulated parasitoids. The results of these studies indicate that the usual innate tendency of released parasitoids to disperse may be overcome to a certain degree by stimulation with kairomones at the time of release. Stabilization and orientation of the parasitoids into a "find and attack" cycle could be achieved. This potential use of kairomones when combined with spraying of host-seeking chemicals is probably mutualistic and could result in additive improvement of the efficiency and performance of parasitoids released in biological control programs.

Treatment of natural and factitious host larvae with kairomones resulted in significantly greater parasitization in the kairomone treated larvae (Table 17). Even unnatural hosts such as Anticarsia gemmatilis (velvet bean caterpillar) and Galleria mellonella (wax moth) were stung and oviposited in after they had been topically treated with kairomonal extract. The treatment of larvae, especially non-host larvae, apparently rendered them more "recognizable" or "acceptable". Vinson (1975a) demonstrated this phenomenon in a study involving the parasitoid, Cardiochilles nigriceps, and 2 factitious hosts, G. mellonella and S. frugiperda. Although eggs were deposited in the 2 unnatural hosts, VBC and WM, subsequent rearing of these larvae did not yield any mature parasitoid larvae. This indicated that these 2 unnatural hosts were either not physiologically suitable or that they possessed defense mechanisms which suppressed the successful development of or encapsulated the parasitoid. If a cheaper, easier to rear, and physiologically suitable factitious host could be made more acceptable to parasitoids by kairomone treatment, then a more economical mass rearing program would be possible. Also, the potential practice of spraying kairomones

Table 17. Parasitization by *A. marginiventris* of natural and factitious host larvae topically treated with a hexane frass extract.

Larvae ¹ tested	% parasitization		% superparasitization	
	Control	Treated	Control	Treated
FAW	53.3Aa	80.0Bb	3.3Aa	6.7Aa
CL	36.7Aa	73.3Bb	0Aa	3.3Aa
VBC	6.7Ac	63.3Bb	0Aa	6.7Aa
WM	0Ad	33.3Bb	0Aa	3.3Aa

Means in the same row and within each % category followed by the same upper-case letter, and means in the same column followed by the same lower-case letter are not significantly different (5% level) as determined by Duncan's multiple range test.

- ¹ FAW = fall armyworm
 CL = cabbage looper
 VBC = velvet bean caterpillar
 WM = wax moth

in the field could render certain contemporary species acceptable to parasitization and if these are physiologically suitable, then, the pest load within the agroecosystem would be further reduced.

GENERAL DISCUSSION

The plant, the insect host and the parasitoid are very important components of a living triad interlocked by vital trophic relationships. A holistic approach to the study of the interrelationships of this triad is likely to be most enlightening. Such a holistic approach appears to be relevant to the study of parasitoid host-finding behavioral sequences. Plants have been shown to have many influences on the parasitoids. For example, the corn plant has been demonstrated to play an important role in the host-finding behavior of A. marginiventris, behavior that also includes response to kairomones produced by its host, the fall armyworm. Description and analysis of this host-finding behavior showed that it can be divided into 4 phases consisting of some 12 or more steps. Several of these steps that make up the "find and attack" cycle are mediated by chemical stimuli acting as releasers of an intensive host-seeking behavior. Host-seeking activities were strongly influenced by a combination of plant and host-related factors.

A petri dish bioassay was developed for studying the response of the parasitoid to short-range or contact chemical cues eliciting host-seeking activities. Several sources of these chemical cues or kairomones were evaluated. Frass and substances of cuticular origin were high in kairomonal activity. Strong responses were also shown by the parasitoid to stipled corn leaf, crushed corn leaf and stipled corn leaf presented in

combination with several host substances. These results support the conclusion that the host-finding behavior of A. marginiventris is influenced by both the plant and the host, and further suggests that the responsible semiochemicals (kairomones) are either synthesized de novo by the host or are present in the host food plants.

Crude kairomonal extracts were prepared by maceration of frass and corn leaves using several solvents. Spraying of kairomonal extract onto corn seedlings resulted in greater activation and retention of released parasitoids, and subsequently more parasitization of hosts. Parasitoids could also be stimulated at the time of release by kairomonal preparations. This brought about stabilization, orientation and retention of the parasitoids in the "search and attack" phase, causing the efficiency of released parasitoids to be improved. Factitious hosts could be rendered acceptable by treatment with kairomones.

Additional work is needed in several areas and new avenues, opened up as a result of the overall scenario presented by these studies, offer new grounds for further scientific investigation. One of the major areas requiring work is the chemical identification of the kairomones implicated as host-seeking stimulants for A. marginiventris. Extraction studies done so far have only scratched the surface of this area. More solvents need to be evaluated and additional extraction techniques need to be developed. Chemical characterization, isolation, purification and identification are important aspects that need to be studied so that the nature of the chemical(s) acting as kairomones are more clearly understood. Studies such as dosage-response relationships, possible habituation of parasitoids to kairomones, temporal stability, effect of

temperature, ultra-violet radiation and other field-environmental parameters on the kairomones are important and need to be investigated.

With the accomplishment of chemical and related studies, the potential uses of kairomones for the augmentation and manipulation of parasitoids can be investigated in greater depth and extent. Relevant areas appear to include:

1. Relationship between spraying pattern and rate, and different host densities.
2. Development of formulations that are effective and non-phytotoxic (the hexane extract was observed to cause some kind of scorching of the corn leaves).
3. Optimal concentrations of kairomones for use as a prerelease conditioning agent.
4. Pilot experiments using kairomones in large field situations.
5. Use of kairomones for improving parasitoid egg distribution.
6. Effect of constant exposure to kairomones on parasitoid longevity and total productivity.
7. Inducing oviposition into artificial media for in vitro studies.
8. Detection and monitoring of parasitoids in the field.

Much interesting research on the kairomones of this host-parasitoid system remains to be done.

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BIOGRAPHICAL SKETCH

Wai-Hong Loke is the eldest son of Mr. and Mrs. Yew-Sum Loke of Kuala Lumpur, Malaysia. He was born on May 16, 1948. Wai-Hong received his primary and secondary education in Georgetown, Penang, Malaysia. After graduating from the Penang Free School with a Higher Certificate of Education (equivalent to the General Certificate of Education, Cambridge, Advanced Level) in 1967, he went on to enroll as an undergraduate in the Faculty of Agriculture, University of Malaya, Kuala Lumpur in 1968.

In 1972, Wai-Hong convocated with honors from the University of Malaya with a Bachelor of Agricultural Science degree. He then worked briefly as a tutor in the university before joining the Malaysian Agricultural Research and Development Institute (MARDI) as a Research Officer in the Crop Protection Research Branch.

Between the years of 1973 and 1976, Wai-Hong pursued the degree of Master of Agricultural Science on a part-time basis. He was officially awarded the degree in 1977. In the same year, he was also successful in being selected by his employers, MARDI, to further his studies overseas for a PH.D. degree. He arrived in Gainesville, Florida, in September of 1977 to begin his studies in the Department of Entomology and Nematology of the University of Florida.

Wai-Hong is a member of the Entomological Society of America, Florida Entomological Society, Entomology and Nematology Students' Organization, and Gamma Sigma Delta. He is married to the former Poh-Chooi Chew of Georgetown, Penang.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



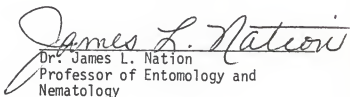
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Associate Professor of Entomology
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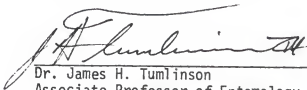
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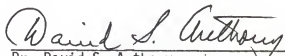
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June, 1981


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